K = calyx; C = corolla; A = stamens; G = ovary; P = perianth;
( ) = joined; ∞ = indefinite; G = superior; Ḡ = inferior; ✿ = Pappus.

Ranunculaceae. K5, C5, A ∞, G ∞.

Rosaceae K5, C5, A 5+5+5 ···, G ∞

Compositeae K0, C(5), A(5), G (2)

Labiatae K(5), C(4), A4, G(2)

Scrophulariaceae K(5), C(5), A4, G(2)

Papilionaceae K(5), C5, A(10)(5+5), G1

Cruciferae K(2+2)(2+2), C4, A2+4, G(2)

Umbelliferae K5, C5, A5, G(2)

Caryophillaceae K(5) C(5), A5+5, G(3 to 5)

Primulaceae K(5), C(5), A5, G(5)

Violaceae K5, C5, A5, G(3)

Liliaceae P3+3, A3+3, G(3)

Orchidaceae P3+3, A1, G(3).

L. Goulding.

March 1925.

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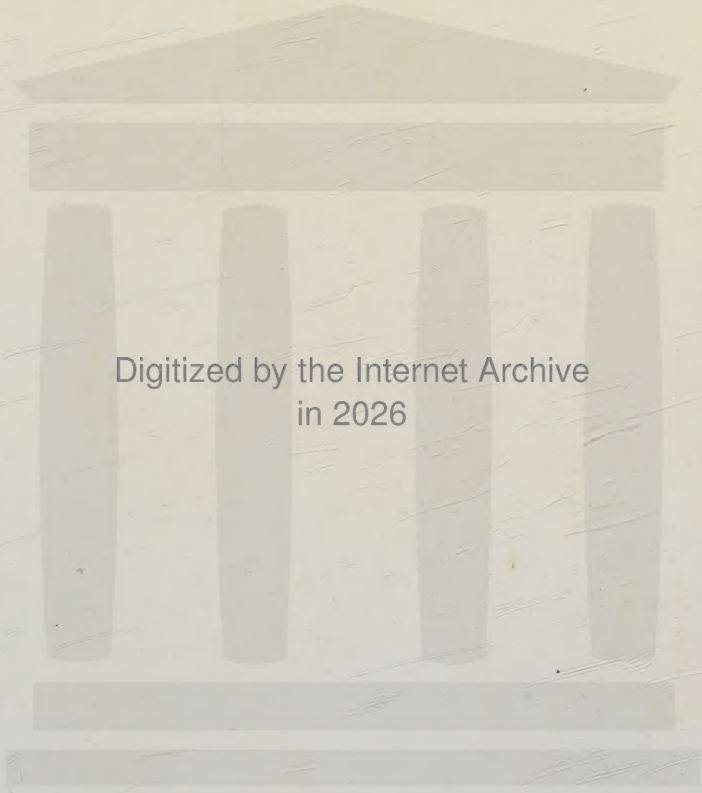

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FIG. 74.—Photograph of a portion of a plant of the Gorse, covered with the thread-like stems of the Dodder (*d*). On these the numerous bunches of flowers (*fl.*) can be seen. [Photo. E. J. S.]

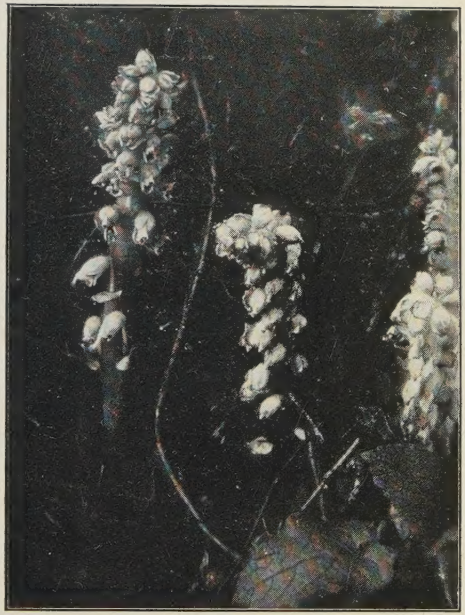

FIG. 76.—Photograph showing three shoots of the Toothwort; each bears numerous flowers. [Photo. E. J. S.]

AN INTRODUCTION

TO THE

STUDY OF PLANTS

BY

F. E. FRITCH, D.Sc., Ph.D., F.L.S.

PROFESSOR OF BOTANY, EAST LONDON COLLEGE,
UNIVERSITY OF LONDON

AND

E. J. SALISBURY, D.Sc., F.L.S.

FELLOW OF, AND LECTURER IN BOTANY AT,
UNIVERSITY COLLEGE, LONDON

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PREFACE

It is hoped that the present volume, for which we are throughout jointly responsible, may supply the need for an elementary introduction to the study of the manifold aspects of plant-life. To fulfil this object we have gone beyond the usual scope of such a book by the inclusion of a chapter on the soil in relation to the plant and a somewhat detailed account of vegetation as a whole. These constitute the essentially novel features. Apart from such additions, which are necessary in the light of present-day requirements and which serve to give the student a broader outlook on his subject, we have endeavoured, wherever possible, to relieve the tedium of mere description by relating form and structure to the functions served. In thus giving considerable prominence to the physiological aspect, we have aimed at demonstrating essential principles by means of simple experiments with inexpensive apparatus.

With few exceptions, only such details of the internal structure of the plant have been included as can be recognised with the help of a good hand-lens; it appears, however, not to be generally realised, how much can be learnt in this way by the choice of suitable material. In general the use of a microscope at too early a stage is to be deprecated, since the student is thereby led to lose sight of the relation which the part bears to the whole.

The process of pollination has been treated at considerable length, since the study of the relation between flowers and insects is of great value for the training of observation. The chapter on different forms of plant-life at the end of the book has been added in order to give a brief epitome of the Vegetable

Kingdom as a whole. To increase the general usefulness of the book, common British plants have, as far as possible, been used as examples, and a very considerable number of wild types are referred to in this way.

The subject-matter more than covers the scope of the Matriculation syllabus of the universities; at the same time, used in conjunction with Scott's *Structural Botany*, it meets the requirements of first-year students.

The illustrations are throughout original, and have been prepared by one of us, with the exception of Figs. 1, 30, 31, 43, 47, 84, 99, 116, 128, 132, 152, and 155, for which we are indebted to Miss E. M. Salisbury, and the photograph on p. 349, which we owe to Mr. W. B. Johnson. To Professor J. T. Hewitt, F.R.S., who has been good enough to read through the chemical matter, we herewith tender our best thanks. We are also under an obligation to the publishers, who have given us every facility in the illustration of this volume. It may be added that great care has been expended in making the Index a complete and reliable key to the contents of the book.

Whilst a considerable number of the experiments described are new, we desire to express our indebtedness to W. J. V. Osterhout's *Experiments with Plants* and to E. J. Russell's *Lessons on Soil* for several suggestions.

F. E. F.
E. J. S.

East London College, *June* 1914.

PREFACE TO SECOND EDITION

In preparing this volume for a second edition we have made but few changes. The most important of these are the introduction of the porometer (p. 369) and the revision of some of the ecological matter rendered necessary by the rapid advances in this branch of our subject.

F. E. F.
E. J. S.

East London College, *August* 1917.

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CHAPTER I

The Plant considered as a Whole

The Vegetable Kingdom includes a great variety of forms, of which some are exceedingly small and simple in structure, whilst others—as, for example, the flowering plants with which we are chiefly concerned in this book—may attain a large size and are relatively complex. The lower and simpler forms of plant-life are illustrated by Seaweeds, Toadstools, Mosses and Liverworts, whilst the higher divisions comprise such types as the Ferns, the Conifers (*e.g.* Scotch Fir, Cedar, Yew, etc.) and the Flowering Plants.

In order to obtain a general idea of the living organism termed a flowering plant we will examine the Shepherd's-purse (*Capsella bursa-pastoris*), which is exceptionally common on waste ground at all times of the year (Fig. 1). It soon appears on exposed soil that is not carefully tended, increasing very rapidly and successfully competing with other plants growing in the same situation. In short, it possesses some of the distinguishing characteristics of a weed and will serve to make us familiar with the broad features of a plant.

Observation teaches us that this, like all flowering plants, has two distinct parts which clearly live under very different conditions. One part, the *shoot*, consisting of the stem bearing leaves (Fig. 1, *Sh.*), is situated overground, being surrounded on all sides by the air and exposed during the daytime to the light of the sun. The other part, the *root* (Fig. 1, *Rt.*), is situated underground, is completely embedded in the soil, and consequently lives in darkness. It is not difficult to find further points of distinction between shoot and root. Thus the parts of the shoot (stem and leaves) are green, whereas the root and

its branches are white. The branches of the root are all similar in appearance, but the stem bears different kinds of branches, some of which are round and slender like itself, while others are broad thin flat structures known to us as leaves. Other differences will become apparent when we have studied these two parts of the plant in greater detail.

On examining the root more closely we find that there is a main portion (Fig. 2, *m.a.*) which is a direct downward continuation of the stem, its position being therefore more or less vertical. This, the main axis of the root, bears side-branches (the *lateral roots*, Fig. 2, *l.r.*[1]) which grow outwards and slightly downwards, so that they stand at an acute angle. In older plants the lateral roots bear further branches (Fig. 2, *l.r.*[2], *l.r.*[3]) which spread out in all directions.

A short distance behind the tips of the main root and its branches careful examination with a lens will show a number of very short colourless hairs (the *root-hairs*) which, however, can be much more readily seen if a plant of the Shepherd's-purse, after washing away the soil, is placed for a day or two with its roots in water (Fig. 2 C, *r.h.*). In the root-system thus treated the extreme tips are seen to be devoid of root-hairs, each being protected by a darker hood-like covering, the *root-cap* (Fig. 2 C, *r.c.*) which is not readily discernible in a freshly uprooted plant. If we scrape the surface of the root with a blunt instrument, we find that the outer part consists of a soft substance, but, if the scraping be continued, we ultimately arrive at a harder central core (Fig. 2 A and B, *c.c.*) which runs the whole length of the root.

We will now turn to a further examination of the aerial part, the shoot. Here again, as in the root, we have to distinguish a vertical main axis (Fig. 1, *a.i.*) bearing lateral branches which, however, grow outwards and upwards. All the lateral branches will be found to arise immediately above a leaf and, since the angle between a leaf and the stem upon which it is borne is termed the *axil* of the leaf (Fig. 3 E, *axil*), the branches are described as axillary (Fig. 1, *ax.b.*, Fig. 3 E, *a.b.*). That part of the stem from which a leaf arises is called a *node* Fig. 1, *n*), whilst the portion between two nodes is spoken of as an *internode* (Fig. 1, *in.*). At the base of the stem a considerable number of leaves generally arise close together

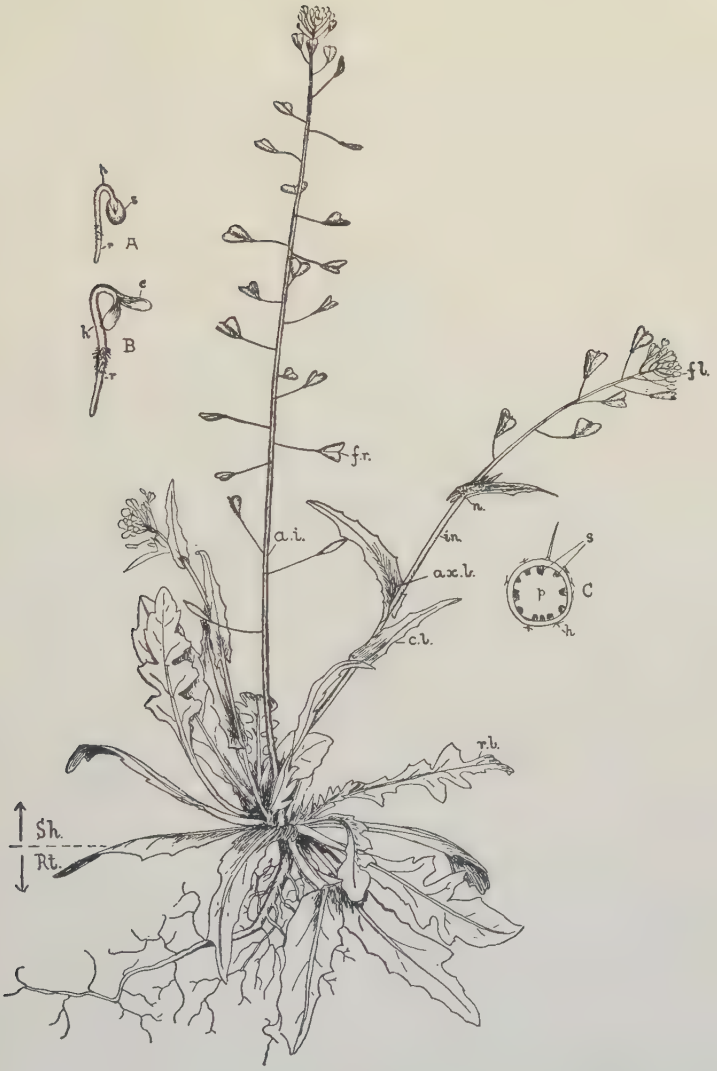


FIG. 1.—Complete plant of Shepherd's-purse (slightly reduced). The surface of the soil is indicated by the dotted line on the left. *a.i.*, axis of inflorescence ; *ax.b.*, axillary bud ; *c.l.*, cauline leaf (see p. 81) ; *fl.*, flowers ; *fr.*, fruit ; *in.*, internode ; *n.*, node ; *r.l.*, radical leaf (see p. 81) ; *Rt.*, root ; *Sh.*, shoot. A and B, Two stages in germination (somewhat enlarged). *c*, cotyledon ; *h*, hypocotyl ; *r*, radicle ; *s*, testa. C, Cross-section of stem (magnified about 8 diameters). *h*, hair ; *p*, pith ; *s*, woody strands.

without perceptible internodes, forming a rosette (Fig. 1) on the surface of the ground, though as the plant grows older this rosette tends to die away.

By scraping away the surface of the stem, in the same manner as in the case of the root, we find that the soft outer part is

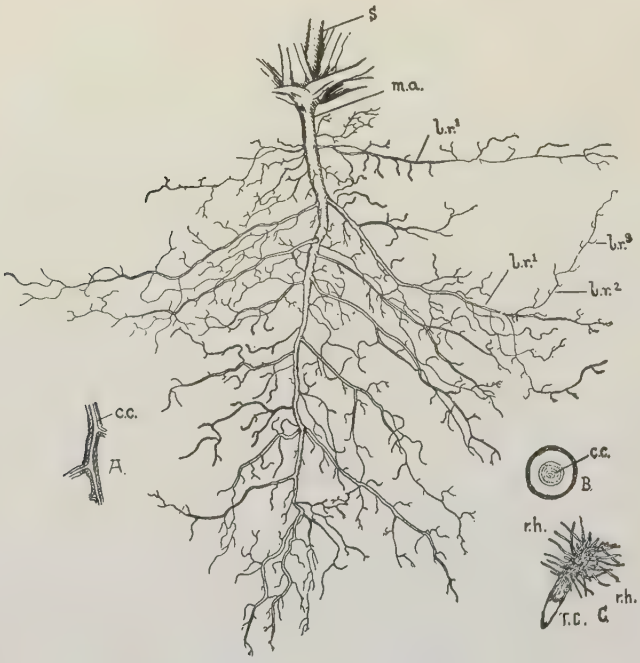


FIG. 2.—Root-system of Shepherd's-purse (natural size). *S*, base of stem ; *m.a.*, main axis of root ; *l.r.*¹, lateral branches of first order ; *l.r.*², laterals of second order ; *l.r.*³, laterals of third order. A, Longitudinal section through portion of main root (about 3 times natural size). B, Cross-section of same (× 6) ; *c.c.*, central core. C, Tip of a root grown in water (× 10). *r.h.*, root-hairs ; *r.c.*, root-cap.

quite a thin layer, and that we almost immediately come to a number of narrow light-coloured threads or strands consisting of harder substance and running lengthwise. On cutting across the stem with a penknife these strands appear as a variable number of pale-green dots (Fig. 1 C, *s*) situated around the edge of the cross-section, whilst the central region is here

occupied by soft tissue (*p*), a marked point of contrast to the root.

In the leaf two parts can usually be distinguished, the leaf-stalk or *petiole* (Fig. 3 B, *pe.*) and the flat part of the leaf, the *blade* or *lamina* (Fig. 3 A, *la.*). The margin of the latter is no regular, but, if we examine a number of plants, all stages from leaves with an almost smooth outline to those in which it is

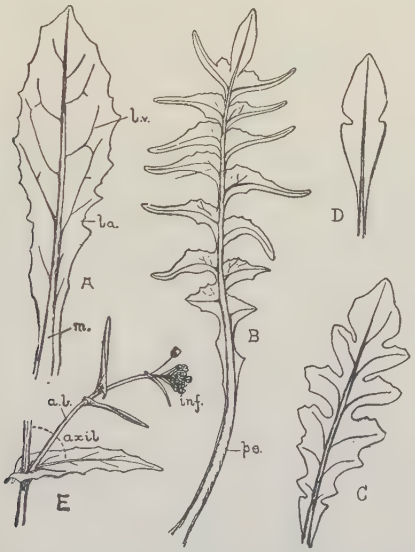


FIG. 3.—A–D, Forms of radical leaves of Shepherd's-purse (about half natural size). *m*, midrib; *la.*, blade; *l.v.*, lateral vein; *pe.*, petiole. E, Node with leaf and axillary branch bearing inflorescence (*inf.*) (about half natural size). *a.b.*, axillary branch.

deeply indented can be found (Figs. 1 and 3). In general the upper leaves are less deeply cut and have a shorter leaf-stalk than those forming the rosette—in fact, most of the upper leaves have no petiole at all (such leaves being described as *sessile*) and the base of their lamina forms two projections enclasping the stem (Fig. 1, Fig. 3 E). The lamina has two surfaces, one of which is directed upwards towards the light, whilst the other faces downwards, and it will be noticed that the upper is darker green than the lower. Extending from the base to

the tip of the leaf and forming a direct continuation of the petiole is a prominent strand, which projects markedly on the under side and is known as the *midrib* or principal vein (Fig. 3 A, *m*). Arising from the latter are a number of finer strands (the *lateral veins, l.v.*) which branch still further to form a network (often difficult to see in the Shepherd's-purse) upon which the delicate substance of the leaf is spread out.

The surfaces of stem and leaves bear numerous scattered *hairs* (Fig. 1 C, *h*). These outgrowths are of a white colour, and whilst some, especially prominent on the edges of the

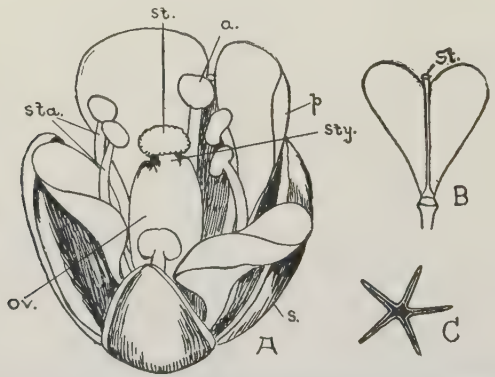


FIG. 4.—A, Single flower of Shepherd's-purse (much enlarged) ; *s*, sepal ; *p*, petal ; *sta.*, stamens ; *a*, anther ; *sty.*, style ; *st.*, stigma ; *ov.*, ovary. B, Single fruit (much enlarged) ; *st.*, stigma. C, Single star-shaped hair from leaf (much enlarged).

leaves, are simple and almost straight, others are branched in a star-shaped manner (Fig. 4 C).

Terminating the main stem and some of its larger branches are clusters or *inflorescences* consisting of small flowers borne on slender stalks (Fig. 1, *a.i.* ; Fig. 3 E, *inf.*). Each flower is composed of the following parts (Fig. 4 A) : On the outside there are four small green or slightly purplish leaves, each of which is called a *sepal* (*s*), whilst collectively they are termed the *calyx* ; next within, and alternating with the sepals, are four larger white leaves, the *petals* (*p*), together known as the *corolla* ; these are followed by six structures called stamens (*sta.*), each of which consists of a short stalk or

filament bearing at its tip a yellowish swelling or *anther* (*a*) covered with a yellow powder, the *pollen*; in the centre of the flower is situated the *ovary* (*ov.*), which appears as a small, green, flattened structure, surmounted by a short peg-like projection, the *style* (*sty.*), which ends in a little knob, the *stigma* (*st.*).

The pollen of the stamens is received by the stigma and, as a result of further growth, the ovary gradually develops into the ripe fruit (Fig. 4 B), during which the stalk of the flower elongates, calyx, corolla, and stamens wither away, and the internodes between the flowers become drawn out (see Fig. 1). On older plants the ripe fruits are seen, in the lower part of the inflorescence, as flat green triangular structures with an apical notch in which the remains of style and stigma can be distinguished (Fig. 4 B). If we split open a ripe fruit we find inside a number of small pale green bodies attached by short stalks and constituting the seeds; these have developed from minute structures (the *ovules*), present in the ovary of the young flower, as a result of changes following upon the reception of the pollen by the stigma.

Older plants, which have been flowering for some time, will show the ripe fruits opening of themselves and shedding the contained seeds, after which the parent sooner or later dies away. The seeds get washed into the soil by the rain and after a brief period give rise to new plants. In this way the Shepherd's-purse not only reproduces its kind, but also multiplies.

Like most plants, the Shepherd's-purse is built up of innumerable small units called *cells*, the detailed structure of which can only be studied with a microscope. These cells are not all of one kind, differing amongst themselves according to the purposes which they fulfil. At the tips of the branches of root and stem are situated groups of very small tender cells, which during the growing period are constantly multiplying by division into two and thus provide the new units by means of which an increase in length takes place. These groups of cells are consequently termed the *growing points*.

Having thus become acquainted with the general structure of the plant, we may now consider the purposes or functions of its different parts or organs. It is obvious that the root in the first place performs the function of fixing the plant in

the soil, as shown by the effort which is often required to uproot it. The efficacy of the root-system in this respect is demonstrated by the difficulty that is experienced, when we attempt to break it, especially by means of a pull ; and it will be seen that this is due to the central core of hard substance with which we have already become familiar (p. 2).

In the stem, on the other hand, the hard strands, as we have seen, are situated round the edge (cf. Fig. 1 C with 2 B), and this arrangement renders the stem more suited to meet bending strains in all directions under the influence of the wind. The leaves which offer a relatively large surface to the wind would of course be particularly liable to become torn, were it not for the fact that the delicate tissue is fully supported by the network of the veins which, with the hard strands of the stem and root, form a continuous skeleton throughout the plant.

The second important function of the root is absorption of water from the soil, a fact which can be simply shown by leaving an uprooted plant lying on the surface of the ground and observing the withering that rapidly ensues. The actual absorption of moisture can be demonstrated by placing a plant of the Shepherd's-purse with its root-system in a tumbler of water, the surface of the latter being covered by a thin layer of oil to prevent evaporation. The level of the water in the tumbler should be marked by a strip of gummed paper, and a perfectly similar arrangement, but without a plant, should be set up beside it to serve as a control. After some hours the level of the water in the tumbler containing the plant will be found to have fallen, whereas no appreciable change is noticed in the control. As we shall learn more fully later on, this absorption of water is actually effected by the root-hairs.

The stem, besides serving to bear the leaves and inflorescences, forms the channel through which the water absorbed by the roots is conveyed to the different parts of the shoot. By cutting off the tips of the roots of a complete plant and placing its root-system in water which is deeply coloured by red ink, the whole course of the water through the plant can be traced. If, after some hours, we split up the main root and stem lengthwise we shall find that the red colour is confined to the hard central core of the root and to the similar strands which run

near the surface of the stem. Moreover, the veins of some or all of the leaves (and even parts of the flower) will be seen to be similarly coloured, thus proving that the continuous skeleton referred to above also serves as the water-conveying mechanism of the plant.

The water which is thus brought to the leaves is not pure, but is a very weak solution of the various mineral substances present in the soil, and many of these are necessary for the nourishment of the plant. Much of the moisture that reaches the leaves is given off from their surface in the form of water-vapour, while a certain amount is retained and built up into the substance of the plant. The continual loss by evaporation from the aerial parts is made good by absorption through the roots. In this way a large body of water passes through the plant, leaving behind its mineral salts, which are thus obtained in sufficient amount for the purposes of nutrition.

The process of evaporation from the leaves may be roughly studied by using filter paper soaked in a solution of cobalt chloride and subsequently dried in an oven or before a fire. Such paper appears deep blue, but readily turns pink and finally almost colourless on exposure to moisture. Leaves of the Shepherd's-purse are placed on a sheet of dry blotting-paper, some with their upper and some with their under surfaces directed upwards. Small pieces of the dry cobalt-paper are then laid on each, and the entire series is covered with a dry sheet of glass to prevent access of damp air. It will be noticed that the pieces of cobalt-paper in contact with the under surfaces of the leaves become colourless more rapidly than those upon the upper surfaces, thus showing that more water-vapour escapes in a given time from the under than from the upper side.

We shall find later that the surface-skin on both sides of the leaf is perforated by a large number of minute holes or pores, which are far more numerous on the under than the upper surface and through which the water-vapour mainly escapes. The plant is able to vary the size of these holes to a slight extent and thus to control the loss of water-vapour. For this and other reasons it is usual to speak of the giving off of water-vapour by the plant, not as evaporation, but as *transpiration*. A diminution in the size of the pores takes place, for example, when the plant begins to wither as a result of deficiency in the

water-supply, so that under these circumstances the amount of transpiration is reduced. This can be shown with the help of the cobalt-paper by comparing the transpiration of a wilted and a fresh leaf.

We have already seen that one of the most striking differences between the aerial and underground parts is the green colouration of the former, particularly of the leaves. The colour is due to a green pigment known as *chlorophyll*, which plays an important part in the nutrition of the plant. If a plant is killed by immersion in boiling water and is subsequently placed in methylated spirits, a solution of the chlorophyll is obtained, leaving the plant itself colourless. If some of the leaves of the latter are now placed in a solution of Iodine (Appendix I.), they rapidly acquire an almost black colour which is a sure test for the presence of starch.

It can easily be shown that starch is only to be found in the leaves after the plant has been exposed for some time to the light. Two similar specimens of the Shepherd's-purse should be planted in separate pots and, whilst one is left exposed, the other is covered over so as to be in darkness. After forty-eight hours a leaf is removed from each plant and decolourised in the way described above. On treatment with Iodine it will be found that the starch-reaction is only shown by the leaf from the exposed plant. We thus see that starch-formation in the leaves goes on only in the presence of light.

If the experiment we have just performed be continued for several weeks, the plant in the dark assumes a starved appearance as compared with the one in the light, so that starch is evidently an important food-substance. It will also be noticed that any new leaves formed in the dark are practically colourless, which shows that light is necessary for the formation of chlorophyll. If such a plant is subsequently exposed to illumination, it will be found that starch soon reappears in the green leaves, but no starch is produced in the colourless leaves until after they have become green. This proves that chlorophyll also is necessary for starch-production.

It will subsequently become apparent that the starch in the leaves of plants is formed, with the help of light and chlorophyll, from the carbonic acid gas (or carbon dioxide) of the air and some of the water which passes into the leaves, the gas obtain-

ing access to the interior through the pores above mentioned. During this process Oxygen is given off. The necessity of carbonic acid gas for the production of starch can be shown by the following experiment.

Two plants of the Shepherd's-purse in pots are kept in the dark until a leaf from each gives no starch-reaction with Iodine. One of the plants is placed upon a glass plate, and soda-lime (Fig. 5, *S.L.*), which absorbs carbon dioxide, is heaped up around the lower part of the pot, the whole being then covered by a bell-jar, whose edge has been previously vaselined to form

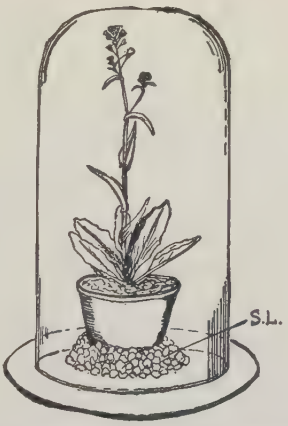


Fig. 5.—Apparatus to demonstrate that a Shepherd's-purse plant does not form starch in the absence of carbon dioxide. *S.L.*, soda-lime.

an air-tight connection (Fig. 5). The second plant, serving as a control, is similarly treated, but no soda-lime is placed beneath the bell-jar, and both experiments are then exposed to bright sunlight. After some hours a leaf is removed from each plant and tested for starch, whereupon it will be found that the one under the bell-jar containing the soda-lime has failed to form starch owing to the absence of carbonic acid gas.

The building up of starch and similar substances from carbon dioxide and water is spoken of as *carbon dioxide assimilation*, and, owing to the part which light plays in the process, the alternative term *photosynthesis* is often employed. This is the first step in the nutrition of the plant and leads on to the

formation of the more complicated substances of which it largely consists and in the production of which the mineral salts absorbed from the soil play a part.

There remains one other important vital process carried on by the plant, viz. the taking in of Oxygen and the giving out of carbon dioxide. This is the breathing process (*respiration*) common to plants and animals. The exchange of gases in this case is just the reverse of what occurs in assimilation, and this latter being a much more active process, respiration is completely masked in the presence of light. Consequently a satisfactory demonstration of the fact that plants breathe can only be obtained in the dark. Place a number of plants of the Shepherd's-purse in a closely stoppered jar, a similar quantity of dead specimens being put into another jar to serve as a control. After forty-eight hours a lighted taper plunged into the jar containing the living plants will be immediately extinguished owing to the absence of Oxygen, whereas it continues to burn in the other jar. Breathing, in fact, is just as essential for the existence of the plant as for that of the animal.

From our study of the plant as a whole we have learnt that the substances requisite for its nourishment are obtained from two sources, viz. the soil and the air. By means of the root the plant is fixed in the ground and absorbs water which contains mineral salts in solution. Most of this water is given off in transpiration, but the remainder, together with the dissolved salts, is retained and contributes to the maintenance of the plant. Through the agency of the chlorophyll in the presence of light chemical changes are brought about, which transform the carbon dioxide and some of the water into food-substances. These together with their further products not only serve for the nourishment of the plant, but supply the material for continued growth. It is in this way that the seedling, living at first on food stored up within the seed, is able to increase in size and finally to form numerous fresh seeds, each capable of giving rise to a new individual. All of these vital processes involve a loss of energy, made good by the energy set free in respiration, and hence its importance for the maintenance of life.

CHAPTER II

Plant-Habit and Duration

A number of our common plants, such as the Poppy, the Sweet-pea, and the Nasturtium, appear above ground in the early spring, arising from seeds that have lain dormant in the soil during the winter. After a period of rapid growth flowers are formed and these, towards the end of the season, produce fruits from which the seeds are eventually shed; subsequently the rest of the plant dies away, and the same sequence is repeated in the following seasons. Such plants, which pass through the whole of their life-history in the course of a single year, are called *annuals*. There are some plants, particularly weeds like the Shepherd's-purse (Fig. 1) and the Groundsel, in which the whole life-cycle occupies a much shorter interval of time, so that several successive generations are produced in the same year. Owing to their rapid growth such plants, which are termed *ephemerals*, readily establish themselves on new ground.

The annual uses up all of its available food-materials in the production of seeds, but if this be prevented by removing the flower-buds as they appear, it may in many cases be induced to survive into a second season. There are, however, a large number of plants which normally in nature require more than a single year to amass the necessary food-materials for seed-formation. Some of these, which are termed *biennials*, flower only in the second year of their life and soon afterwards die away; examples are furnished by the Mullein (Fig. 6), Canterbury Bell and the Carrot. Such plants during the first season's growth do not get beyond the production of a rosette of leaves close to the surface of the ground (Fig. 6 B). The food-substances formed by these leaves pass into the sub-

terranean portion, which becomes somewhat swollen and serves as a storage-organ (Fig. 30 A, p. 56). During the ensuing winter the plant remains in a dormant condition, the leaves, since they lie in close proximity to the soil, obtaining a certain amount of protection by surrounding vegetation and inequalities of the surface of the ground. In the following year rapid

FIG. 6.—The Mullein, a biennial (greatly reduced). B, In the rosette-stage (first year). A, In the stage found in the second year.

growth takes place, largely at the expense of the food stored up in the underground parts, and as a result a tall stem bearing a mass of flowers is produced (Fig. 6 A). Under certain circumstances, such as growth on very poor soil, the biennial will be found to form a few flowers and seeds already in the first year and then to die away, thus behaving like an annual.

We can readily imagine a biennial in which the vitality of the plant is not completely exhausted by the production

of flowers and fruits, so that sufficient food-material remains to support renewed growth in the following spring. If this goes on from year to year we should obtain a so-called *perennial*, and a large number of plants in nature persist in this manner. As instances we may mention the Stinging-nettle, the Dog's-mercury, the Perennial Sunflower, the Crocus (Fig. 90, p. 160) and the Solomon's Seal. If such plants are grown from seed, some will be found to flower already in the first year, whilst most require two or even more years to attain to sufficient vigour before flowers are produced; meanwhile they are accumulating a store of food in their underground organs (Figs. 88 and 89 A, pp. 157, 158).

In the examples above mentioned the aerial parts die down at the end of each season, whilst the subterranean parts (the corm in the case of the Crocus, the stem in the case of the Solomon's Seal) persist and by virtue of their store of food-material are able to produce new shoots in the following spring. When the plant begins to form flowers, it is sufficiently vigorous to provide the necessary food for the resulting seeds, and yet to transfer enough into the underground organs for the commencement of next year's growth. A few perennials of the type we are considering, such as the Dandelion or Iris, always retain some of their leaves even during the winter, although in other respects they behave exactly like those we have described.

The kinds of perennials hitherto noticed are called herbaceous perennials, since they produce no permanent overground shoot-system. In contrast to these, however, a large number of perennials, namely shrubs and trees, form stems which become hard and woody and consequently persist to form the starting-point for each year's growth, a feature that enables them to attain in many cases to very considerable dimensions. In the British flora such woody *perennials* are confined to one of the two great subdivisions of flowering plants, the so-called Dicotyledons (cf. p. 34), although this habit is also found among the Conifers (*e.g.* Scotch Fir, Yew, etc.). Even in these forms some part, as a general rule, dies back on the approach of winter, as is seen in the falling of the leaves of plants like the Beech, Oak, Briar, Hawthorn, etc., which are consequently described as *deciduous*. A few others, such as

the Holly and the Scotch Fir, are *evergreen*, bearing leaves at all times of the year.

The store of food in these woody perennials is laid down throughout the woody portion of the plant and is here again responsible for the rapid sprouting which takes place with the advent of spring. Trees and shrubs, the two kinds of woody perennials, are distinguished by the fact that the former have a prominent main trunk on which the smaller branches are borne, whilst shrubs have a number of nearly equal main stems arising side by side.

The form of food-reserve in perennial plants is commonly starch, a fact which may be easily verified by cutting open the underground stem of the Iris or Crocus or a thick branch of the Horse Chestnut in winter, and applying the Iodine-test (see p. 10). In other cases (*e.g.* the Solomon's Seal and the Dandelion) forms of food-materials not giving this reaction are found, but a further consideration of these must be deferred till later.

We may finally enquire as to the reason why so many plants die back to a varying extent on the approach of winter. During this period the temperature of the soil is often so low that absorption of water by the roots practically ceases. If, under these circumstances, the plant were to lose water in transpiration (p. 9) at the same rate as in the warmer period of the year, it would soon wither and die. It is to avoid this evil that the leaves are shed or the whole overground shoot-system dies away, the transpiring surface being thereby reduced as much as possible. At first sight the evergreen would appear to be an exception to this rule, but it will be noticed that all evergreen leaves (*e.g.* the Laurel and the Holly) are of a leathery texture, due to an unusually thick surface-skin. As a consequence, transpiration from such leaves goes on slowly at all times of the year, and such little absorption as occurs during the winter is sufficient to replace this loss. It is instructive in this connection to compare the relative rates of transpiration of a deciduous and an evergreen leaf by the aid of the cobalt-method (p. 9).

Plants exhibit a number of diverse habits, of which the erect is by far the most frequent; in this type the aerial shoot-

system is so constructed as to be able to support itself, and examples are furnished by all the plants we have as yet mentioned. It is natural to ask why these plants constantly assume the erect position in nature, and the question may be answered in the following way. If an erect plant be placed next to a window, so that it receives one-sided illumination, the shoot will soon be found to have curved over towards the light (Fig. 7 B). When this has occurred the plant should be turned round through half a circle, whereupon after a

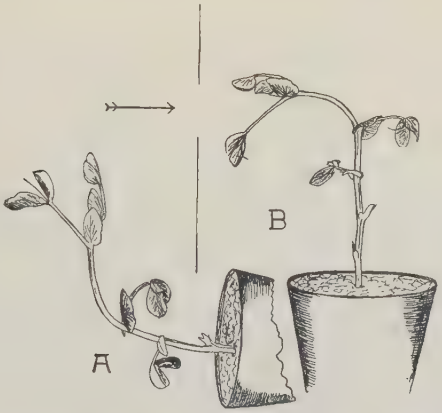


FIG. 7.—A, Seedling of Pea, placed horizontally in the dark, showing the shoot bending up under the influence of gravity. B, Ditto, placed vertically and showing a heliotropic curvature under the influence of one-sided light, whose direction is indicated by the arrow. (About one-third natural size.)

further interval the shoot will again bend over towards the window. We thus see that the erect growth of the stem is dependent on its being exposed to equal illumination on all sides, and that one-sided light causes a bending until this state of affairs is attained. The influence of light upon the direction of growth of the plant is spoken of as *heliotropism*.

It is not difficult to show that other influences play a part in determining the erect position of the shoot, for if we place a potted plant horizontally in the dark for some hours the tip of the shoot gradually curves upwards till it again assumes a vertical direction (Fig. 7 A); the same thing may be fre-

quently observed in nature, when a plant without being uprooted is blown over by the wind, or a branch sinks down as a result of its own weight. In the plant placed in darkness some agency other than light is evidently at work and, as we shall only be able to understand fully later on, this is the force of gravity which in this case has the peculiar effect of causing growth in a direction opposite to that in which gravity acts. The influence of this force on the direction of growth of the plant is termed *geotropism.*

A word or two may be added on the advantages of the

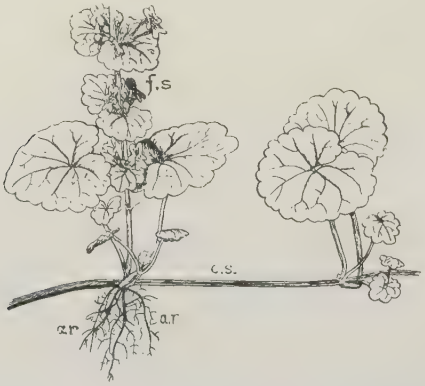


FIG. 8.—Creeping stem (*c.s.*) of the Ground Ivy, showing adventitious roots (*a.r.*) and an erect flowering shoot (*f.s.*) (about half the natural size). The flowering shoot is not shown at its full length.

erect habit. In the first place, the leaves are thus well exposed to the light and most suitably placed for assimilation (p. 11). In addition, the flowers are displayed to the best advantage, a point of great importance, since many plants depend upon insects for the transference of the pollen from the stamens to the stigma. Moreover, the consequent height above the ground greatly facilitates the dispersal of the seeds where, as is frequently the case, this depends upon the action of the wind.

In marked contrast to the erect forms are those plants which assume a creeping habit, as for example the Creeping Jenny, the Marsh Pennywort and the Sea-milkwort. In these

the influence of light and gravity on the direction of growth of the shoot must obviously be a different one. The main advantage of this habit lies in the rapidity with which the plant can cover a considerable surface, whilst the close proximity to the soil entails less exposure to atmospheric conditions. On the other hand, such plants run the risk of being smothered by surrounding vegetation and forgo all the advantages which the erect habit brings with it. These drawbacks are to some extent minimised in certain creeping forms (*e.g.* the Ground

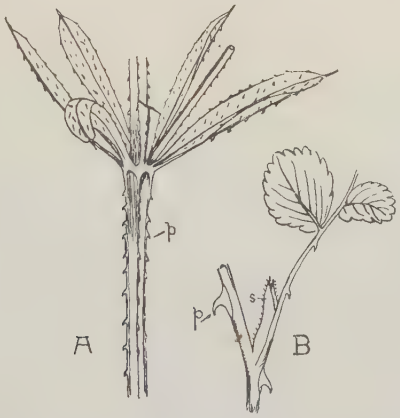


FIG. 9.—A, Portion of shoot of Goose-grass (natural size), to show the prickles (*p*). B, Dog-rose (slightly reduced), with prickles on stem and leaf (only a portion of the latter is shown). *s*, stipules.

Ivy, Fig. 8) by the production of erect flowering shoots from the axils of the leaves of the creeping stem.

There are still other plants which have the tendency to grow erect, but after reaching a certain size are unable to maintain this position unless they find some additional means of support which in nature is generally furnished by the surrounding vegetation. These *climbers* exhibit diverse methods of utilising such aid. The simplest type is afforded by plants like the Goose-grass (Fig. 9 A), the Dog-rose (Fig. 9 B) and the Bramble (Fig. 86, p. 155), which grow vertically for a short time and then, bending over under their own weight, find a suitable support usually in the taller-growing shrubs round about.

The apex of such a *scrambler* always tends to grow vertically upwards under the influence of light and gravity but, in the absence of any prop, the stem sooner or later falls on to the ground after which the younger portion again turns upwards; this is repeated until some support is found, whereupon the erect part of the stem, in the course of its further growth, is raised above the surface of the soil. In the cases we have mentioned the shoot is provided with curved prickles (Fig. 9, *p*), all of which have their tips directed downwards, so that the plant becomes hooked on to its means of support. In the

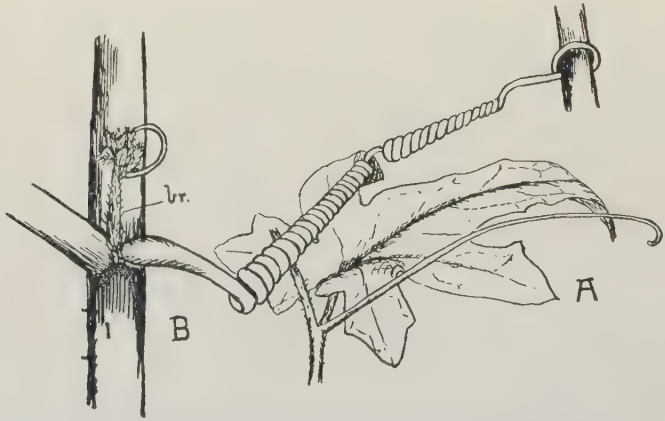


FIG. 10.—Tendrils of the White Bryony (natural size). A, before, B, after clasping the support. *br.*, branch.

Bramble and Dog-rose (Fig. 9 B) these structures are very conspicuous, but in the Goose-grass (Fig. 9 A) they are much smaller, though in general more numerous. Many weak-stemmed plants (*e.g.* the Stitchwort, the Wood Sandwort), which grow more or less erect when they occur in masses, frequently behave as scramblers, if opportunity serves, but do not possess any very marked equipment for this purpose.

Examples of a more elaborate type of climbing mechanism are furnished by those plants which develop special clasping organs or *tendrils*, such as are found in the Sweet-pea (Fig. 123 B, p. 217), the White Bryony (Fig. 10) and the Grape Vine. These tendrils appear as long naked green threads (Fig. 10 A) which,

on contact with a branch or twig, twine round it (Fig. 10 B) and in this way the plant, as it grows, becomes attached to its support. These special climbing organs will be considered more fully in Chapter XVII.

A third method of climbing is adopted by those plants in which the stem itself twines around the supporting object, as is the case in the Convolvulus, the Runner-bean and the Hop

FIG. 11.—Twining stem of Hop (about half the natural size), showing small leaves and long internodes of apical portion. Direction of twining indicated by the arrow.

(Fig. 11). The shoot here at first grows erect, but after attaining a certain height the tip bends over and commences to revolve in a circle (as indicated by the arrow in Fig. 11), a movement which helps the plant to find a foreign object around which to coil. It will be noticed that in these *stem-twiners* the apex of the shoot bears very small leaves (Fig. 11), which soon become separated by remarkably long internodes. As a result of this arrangement twining is accomplished before the leaves are

sufficiently large to interfere materially with the encircling of the support. In the case of the Hop the grip of the climbing stem is greatly aided by the presence of curved prickles similar to those of the scramblers above considered.

There are other methods of climbing, as for instance that of the Ivy by means of roots (Fig. 31, p. 57), but the examples we have noticed are sufficient for the present to illustrate the habit of such plants. The ultimate object of the climber is

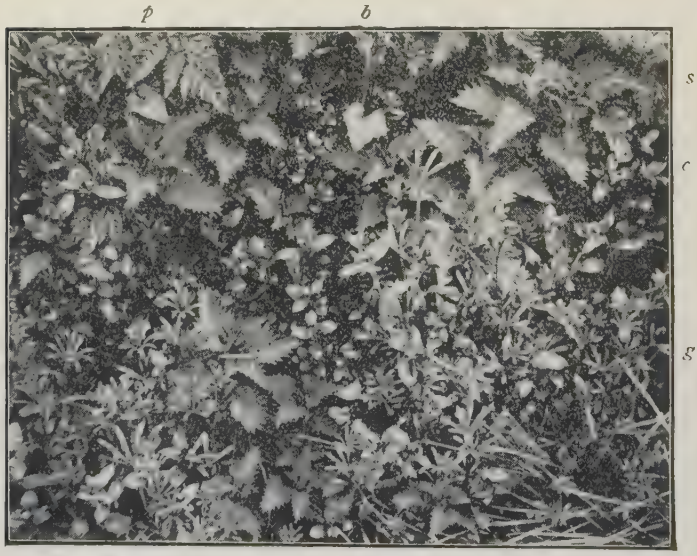


FIG. 12.—Photograph of foot of hedge-row, taken close at hand. *b*, White Bryony; *c*, Chickweed; *g*, Goose-grass; *p*, Beaked-parsley; *s*, Stinging Nettle.

the same as that of the erect plant, viz. the exposure of its leaves to adequate illumination, the display of its flowers in a conspicuous position and the placing of its fruits in a situation aloft suitable for seed-dispersal. This type of habit is in nature found more particularly amongst the dense vegetation of hedges (Fig. 12) and thickets, where competition is keen and adequate means of support are available, typical instances being furnished by the Honeysuckle and the Black Bryony. The climber enjoys the advantage of being able to do without so elaborate

a supporting skeleton as that required by the ordinary erect plant, using the material thus economised for the purposes of rapid growth and the formation of abundant flowers and seeds ; on the other hand, its existence turns on the finding of a suitable support and, if this fails, it has little chance of surviving.

Our brief review of the various types of plant-habit has led us to recognise that each has its own advantages, especially in relation to the conditions which obtain in nature. In every case form and duration are subservient to the adequate nourishment of the individual, its reproduction and consequent multiplication. We can see that advantages on the one hand are, however, balanced by disadvantages on the other. Thus, if the perennial be able to produce numerous seeds year after year, it also requires a relatively long period of preparation. Most woody perennials therefore tend to disappear where browsing animals are plentiful, and annuals alone can successfully thrive in cornfields or on other disturbed soil.

CHAPTER III

Dicotyledonous Seeds and Seedlings

We have seen that, as in the Shepherd's-purse, most flowering plants sooner or later in the course of their life produce fruits and seeds which represent the culmination of each season's growth. Having become detached from the parent-plant in one way or another, the seeds eventually come to lie on the rugged surface of the soil. By the action of the summer's heat and winter's frost the soil becomes broken up, and into the numerous cracks and crevices thus formed the seeds find their way. Burrowing animals, especially Earthworms, contribute to this process of disintegration and, since in the course of their nutrition considerable quantities of soil are passed through their bodies and become deposited at the surface, they constantly transfer earth from below upwards. In rainy weather the little streams of water that percolate into the ground wash the seeds still deeper, whilst at the end of each season's growth fallen leaves and other vegetable *débris* accumulate on the top of the soil and thus afford added protection to the seeds below. In these various ways the seeds become buried at some slight depth in the soil.

As a general rule the seeds remain dormant in the ground until the following spring, when conditions become favourable for their sprouting or *germination*. It is easy to show that seeds only germinate when provided with sufficient moisture and warmth and an adequate supply of Oxygen for breathing. The effect of moisture can be demonstrated by planting seeds of the same kind in half a dozen small (3 in.) pots filled with dry soil or sawdust; the first pot receives no water, the second is given a small amount (*e.g.* 3 c.c.) each day, the third double as much as the second, and the remainder in correspondingly

increasing amounts, so that the last pot receives daily 48 c.c. It will be found that the seeds in the first three pots either fail to germinate or do so (in the case of the third) only after a long interval, whilst those in the fourth and fifth soon begin to grow. The seeds in the last pot may in some cases be found not to germinate so rapidly as those in the preceding two, which is due to the large quantity of water added displacing the air from the spaces between the particles of the sawdust or soil, so that respiration is hindered.

The importance of Oxygen during germination can be more definitely established by placing similar seeds in ordinary water and in water which has been thoroughly boiled and subsequently cooled. In the latter case no growth occurs, consequent upon the removal of Oxgyen by boiling.

In nature, the supply of water and Oxygen are as a rule sufficient for the germination of seeds, and it is the low temperature of the soil that delays this process until the spring. If soaked seeds are planted in three pots of sawdust, one being placed in a cold room (or in summer surrounded by ice), the second in a moderately warm room and the third about a yard from a fire or radiator, all being sufficiently watered, it will be found that the higher the temperature the more rapidly does germination ensue.[1]

Most seeds, even if placed under suitable conditions, will not germinate immediately after being shed, but require a longer or shorter period of rest. In a number of plants which flower and form their seeds early in the season (*e.g.* the Field Speedwell and the Poppy) this dormant period is over by the late summer or autumn, and in such cases germination mostly takes place at this time of the year, the young plants remaining small and passing through the winter in a more or less resting condition.

We may now study the outward characters of some common seed such as that of the Runner Bean (Fig. 13 A). We notice that it is more or less kidney-shaped and is covered with a smooth, tough skin, the seed-coat or *testa*. Along the middle of one of the long edges of the seed there is a narrow white scar (the *hilum*, *h*) which marks the point at which the seed was attached to the pod. At one end of the hilum

[1] The seeds placed on ice will probably not germinate at all.

are two minute swellings (*s*) side by side, whilst near the opposite end is a very small hole (the *micropyle*, *m*) situated at the base of a slight depression.

Some of these seeds may now be put to soak in tepid water and the changes which they undergo observed at half-hourly intervals. We first note a wrinkling of the seed-coat in the neighbourhood of the micropyle, a process which gradually spreads from this region and extends over the whole surface. Still later this wrinkling slowly disappears and the testa again becomes smooth, the seed having now increased to about double its original size. The explanation of these changes lies in the fact that water is first absorbed into the seed-coat at the micropyle and from there diffuses slowly throughout the testa, which consequently swells up. Since the contents of the seed do not at this stage take up water nearly so rapidly, they show little increase in size, so that the enlarging testa is thrown into numerous folds. Subsequently the seed-contents also absorb water vigorously and swelling up gradually fill out and finally burst the surrounding testa. This swelling is accompanied by the exertion of considerable force, which can be shown by filling a narrow-mouthed glass bottle with dry Beans and placing it in a vessel of water; the seeds, as they swell, become more and more tightly packed, until eventually they burst the glass. This principle is in fact often employed for the purpose of removing dents in tin cans, etc.

The micropyle can be shown to be the most important channel for the absorption of water in the following way: Select two dozen dry Beans and seal up the micropyles of half of them with rubber solution; each set of twelve Beans is then weighed separately and placed to soak for twenty-four hours; at the end of this period their surfaces are carefully dried, and each set is reweighed. The result will show that the untreated seeds have increased considerably more in weight than those in which entry of water through the micropyles was impeded (see Appendix II.).

For the examination of the seed-contents it is most convenient to use seeds which have been previously soaked, although the same features could be made out in the dry condition. On removal of the testa two cream-coloured

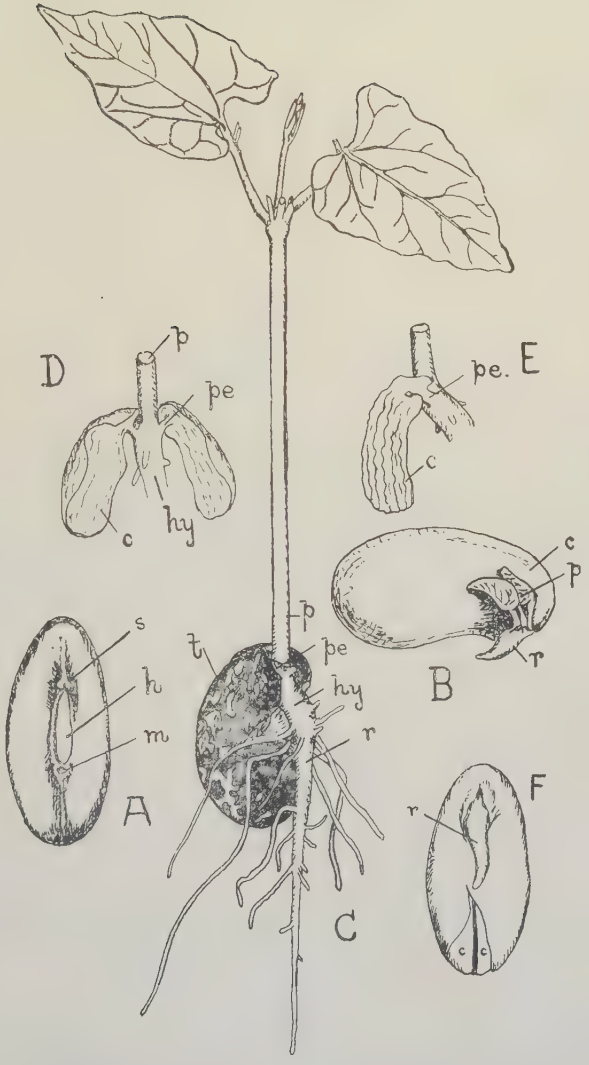


FIG. 13.—Stages in the germination of the Runner Bean (all natural size). A, Soaked seed seen edge on, to show the hilum (*h*), the micropyle (*m*), and the swellings (*s*). B, Seed with testa and one cotyledon removed to show plumule and radicle. C, Mature seedling. D, Partially shrivelled cotyledons, showing attachment to base of plumule. E, Ditto from side, with completely shrivelled cotyledon. F, First stage in germination. *c*, cotyledon ; *hy.*, hypocotyl ; *p*, plumule ; *pe.*, stalk of cotyledon ; *r*, radicle ; *t*, testa.

fleshy lobes, the seed-leaves or *cotyledons*, are disclosed (Fig. 13 B, *c*). If the two cotyledons be carefully separated, a small bud bearing minute yellowish-green leaves (the *plumule* or primary shoot, Fig. 13 B, *p*) will be seen lying between them near to one edge. A close scrutiny shows that each cotyledon is attached to the base of the plumule by a very short stalk or petiole, whilst beyond this point the axis of the plumule is prolonged into a short tapering outgrowth, the *radicle* or primary root (*r*). Whereas the plumule is completely hidden between the cotyledons, the radicle after removal of the testa is seen as a projection lying against their edges (cf. Fig. 13 B). The young plant, which we have thus found within the seed, is termed the *embryo* and includes three types of organs, viz. the radicle, plumule and cotyledons.

It will be noticed that the tip of the radicle fits into a short pocket which arises from the inner surface of the seed-coat and leads down to the micropyle. This pocket acts like the wick of a lamp in drawing up moisture from the soil and passing it on to the radicle, so that this is the first part of the embryo to receive water and swell to a considerable size. As a result it is here that the pressure upon the seed-coat is most pronounced and that the bursting of the testa begins. The radicle, thus freed, grows rapidly downwards (Fig. 13 F) and very soon side-roots arise from it, so that the young plant becomes firmly anchored in the soil. In the meantime the stalks of the cotyledons are slowly increasing in length (Fig. 13 D, *pe*) and, since the cotyledons themselves remain firmly embedded in the seed on the one hand and the root is fixed in the soil on the other, this elongation has the effect of carrying out the plumule clear of the seed-coat (Fig. 16 A). Up to this time the plumule has altered little in size, but now a rapid growth in the upward direction begins. It will be seen that, until after the surface of the soil is reached, the tip of the plumule remains sharply curved, so that it is the more mature region that pushes its way through the ground, dragging after it the young tender leaves at the apex, for which a passage is thus created. This curvature rapidly straightens out after the plumule comes above the surface of the soil into the light (Fig. 13 C).

The early stages of germination are accomplished in dark-

ness, and as a consequence the seedling is unable to manufacture starch and similar food-materials (cf. p. 10). As a matter of fact the early growth of the embryo takes place at the expense of food-substances which became stored up within its cotyledons, whilst the seed was still attached to the parent-plant. The bulk of this food consists of starch, and its presence can therefore be demonstrated by breaking across a cotyledon and applying

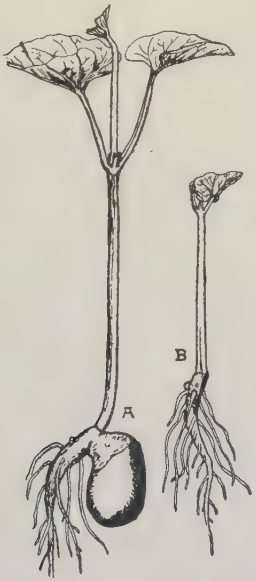


FIG. 14.—A, Normal seedling of the Runner Bean. B, Seedling of the same age, from which the cotyledons were removed at an early stage of germination. (Both about half the natural size.)

Iodine to the exposed surface. If seedlings are examined at successive stages of germination, it will be seen that, as growth proceeds, the cotyledons shrivel up more and more (Fig. 13 D and E) until finally but a shrunken remnant is left. It will thus be apparent that in the Runner Bean the cotyledons are merely storehouses for nourishment and never come above the soil, though, as other examples will show, they do not always behave in this way.

An experimental demonstration of the great part played by the food-reserves in early stages of germination is furnished by cutting off the cotyledons from a number of seeds in which the radicles have obtained a hold upon the soil, care being taken not to injure the remaining part of the embryo in any way. A comparison of normal seedlings with those from which the cotyledons have been removed will show how great an asset this store of nourishment is to the plant (Fig. 14).

As a second example of a seed we may take that of the Castor Oil plant (Fig. 15 A). Neither the hilum nor the micropyle are visible on the testa (*t*) in this case, owing to their being covered by a warty outgrowth (the caruncle, *car.*), which arises late in the development of the seed. By splitting the latter lengthwise in the plane of flattening and examining the exposed surfaces of the two halves a thin white leaf-like structure showing midrib and lateral veins will be seen on each (Fig. 15 B, *c*). These are the cotyledons which in this case are very thin and only occupy a small portion of the seed-contents (Fig. 15 C, *c*). On one half or the other, at the narrower end of the seed, will be found a small white peg (Fig. 15 B), the pointed end of which lies nearest the caruncle and constitutes the radicle (*r*), whilst the opposite blunt end represents the plumule (*p*). The stalks joining the cotyledons to the base of the plumule are in this case so short as to be hardly recognisable (see also p. 35).

We thus see that the embryo of the Castor Oil seed, while showing the same organs as that of the Bean, is much less developed in the resting condition. A further distinction lies in the fact that the embryo of the Castor Oil only occupies part of the seed and that it is completely surrounded by a white fleshy mass, the *endosperm* (Fig. 15 B and C, *e*), which is all that one sees when the seed-coat is removed. This is a tissue containing food-reserves for the nourishment of the young plant, and the chief difference from the Bean is therefore that in the latter the food-substances are stored up *in the embryo itself*, whereas in the Castor Oil there is this special food-tissue *outside the embryo*. Since the endosperm is sometimes spoken of as the albumen, seeds which possess this tissue are said to be *albuminous*, whilst those lacking it (*e.g.* the Bean) are described as *exalbuminous*. Treatment of a broken surface

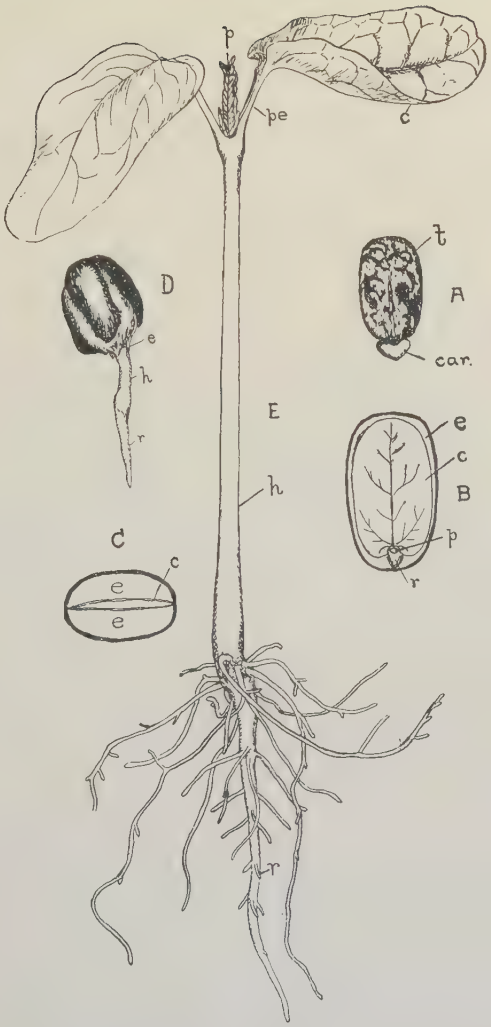


FIG. 15.—Structure of seed and germination of Castor Oil plant (A, D and E natural size, the others enlarged). A, Entire seed. B, The same halved lengthwise. C, Ditto, cut across. D, First stage in germination. E, Mature seedling. *c*, cotyledon ; *car.*, caruncle ; *e*, endosperm ; *h*, hypocotyl ; *p*, plumule ; *pe.*, petiole of cotyledon ; *r*, radicle ; *t*, testa.

with Iodine will show that starch is not present in the endosperm of the Castor Oil seed, its place being taken by the oil which is used medicinally.

The first result of placing seeds of the Castor Oil to soak is that the caruncle which sucks up water like a sponge increases in size and becomes softer. The seed-coat in this case is so rigid that practically no swelling of the seed as a whole is observed and, since the water absorbed by the caruncle is passed on to the adjacent radicle, this part of the embryo is again the first to swell up, leading to a rupture of the testa at this point. The radicle grows downwards into the soil (Fig. 15 D) and begins to form lateral roots whereby, as in the case of the Bean, the young plant becomes fixed. If a slightly older seedling is examined (Fig. 16 B), it will be noticed that prominent elongation is taking place in a region of the axis situated between the place of origin of the lateral roots and the point of attachment of the cotyledonary stalks. This elongating region has a reddish tinge in contrast to the white root and represents a portion of the stem situated *below* the cotyledons, for which reason it is spoken of as the *hypocotyl* (Fig. 16 B, *h*). Such a hypocotyl is present also in the Runner Bean (Fig. 13 D, *hy*), but remains so short that it is difficult to recognise.

The rapid growth of the hypocotyl in the Castor Oil results in its becoming arched upwards (Fig. 16 B), and very soon the top of this arch appears as a loop above the surface of the soil. Subsequent to this the hypocotyl begins to straighten as a result of its further growth, and consequently the cotyledons with the plumule enclosed between them are dragged out of the ground (Fig. 15 E).

If a seed be examined a little time before the cotyledons emerge, the endosperm will be found to have nearly disappeared. During their long sojourn beneath the surface the cotyledons are occupied in absorbing food from the endosperm for the growth of the seedling, and throughout this period are undergoing a great increase in size, so that when they come above the ground they are many times larger than in the resting seed and have pronounced petioles (Fig. 15 E, *pe*). As the hypocotyl becomes erect the cotyledons spread out their blades (which have meanwhile developed chlorophyll) to the light (Fig. 15 E), and now serve as assimilatory organs for the young

plant; subsequently by the growth of the plumule other leaves develop to take their place and the cotyledons drop off.

The method of liberation of the plumule from the seed is obviously quite different in the two cases we have studied (cf. Fig. 16), for, whilst in the Runner Bean this is effected by elongation of the cotyledonary stalks, in the Castor Oil it is the lengthening of the hypocotyl that fulfils this purpose. In both cases the delicate tip of the plumule does not push its own way

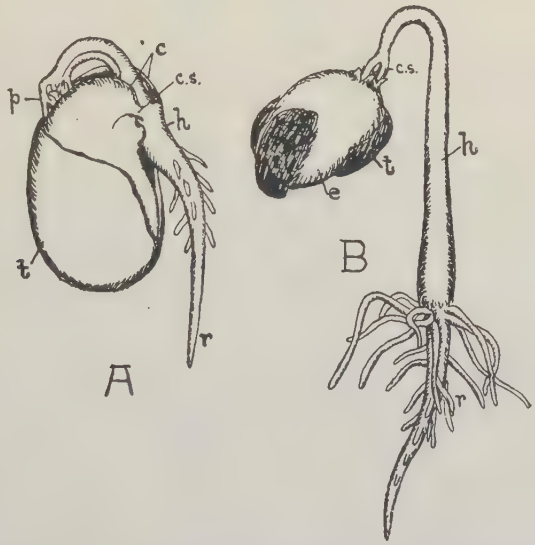


FIG. 16.—Liberation of plumule in A, the Runner Bean; B, the Castor Oil (about natural size). *c*, cotyledons; *c.s.*, cotyledon-stalk; *e*, endosperm; *h*, hypocotyl; *p*, tip of plumule; *r*, radicle; *t*, testa.

through the soil, this being accomplished either by the older part of the plumule or by the hypocotyl; in the case of the Castor Oil the risk of injury by friction with the soil-particles is still further reduced owing to the inclusion of the plumule between the cotyledons during its passage through the ground. Another difference between Runner Bean and Castor Oil lies in the behaviour of the cotyledons, since in the former they remain permanently underground and are said to be *hypogeal*, whilst

in the latter they eventually appear above the surface and are described as *epigeal.*

The two types of seed-structure and germination described in this chapter are characteristic of a large number of flowering plants which, owing in part to their possession of embryos with two cotyledons, are grouped together under the name of Di-

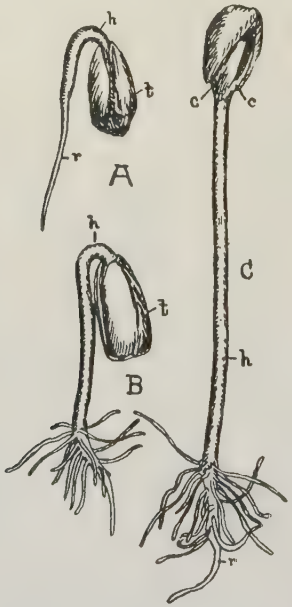


FIG. 17.—Germination of Sunflower (natural size). A, First stage, showing escape of radicle and commencement of elongation of hypocotyl. B, Later stage. C, Hypocotyl straightened and cotyledons preparing to escape from the seed-coat. *c*, cotyledon; *h*, hypocotyl; *r*, radicle; *t*, combined fruit-wall and testa.

cotyledons. As further examples of exalbuminous Dicotyledonous seeds with hypogeal cotyledons we may mention the Pea and the Acorn, but it may be well at this point to draw attention to the fact that there are also exalbuminous seeds with epigeal cotyledons, as, for instance, the Vegetable Marrow, the French or Kidney Bean, the Shepherd's-purse (Fig. 1 A and B) and Sunflower (see Fig. 17); in such cases the cotyledons

remain within the seed until most of their food-material has been absorbed. In the same way albuminous seeds may have either hypogeal or epigeal cotyledons; the latter, as we have seen, occur in the Castor Oil, though examples of the former are very rare amongst Dicotyledons. Since the hypocotyl is mainly responsible for bringing the cotyledons above the surface of the soil, it is always well developed in epigeal seedlings, whilst in the hypogeal types it generally remains short.

Note.—In view of the difficulty often experienced in obtaining seeds of the Castor Oil plant, it may be found convenient to use Buckwheat, which affords an example of the same type of germination. The dry fruit of the latter has three prominent ridges and exhibits, at the broader end, the remains of the floral leaves. When cut across the middle the white endosperm is seen occupying the greater part of the interior, whilst the cotyledons appear as an irregular yellowish line. If cut lengthwise, the body of the embryo may also be seen towards the pointed end of the fruit, with the radicle directed outwards. Here, too, the cotyledons are recognisable as a wavy line.

CHAPTER IV

Monocotyledonous Seeds and Seedlings

Hitherto we have been considering seeds with two cotyledons, but a large number of flowering plants, of which the Grasses and the Lilies furnish examples, possess embryos having but a single cotyledon. For this and other reasons such plants are grouped together as Monocotyledons and with the Dicotyledons form the two great subdivisions of flowering plants. Apart from the difference in the number of cotyledons, however, the embryo of Monocotyledons shows the same essential organs as that of Dicotyledons. In the former group, moreover, both exalbuminous and albuminous seeds are found, although the latter type is by far the most common.

As a first instance of a Monocotyledonous seed we may study the grain of the Maize. We select this Grass owing to its large size, but any one of the Cereals (*e.g.* Wheat, Barley, Rye, etc.) would on a smaller scale show the same essential structure and mode of germination. Examining first the dry grain (Fig. 18 A), we notice that one end, the former point of attachment to the cob, is more or less tapering whilst the other is broad and rounded, two sides of the grain being generally somewhat flattened. On one of these flat faces a whitish oval depression (*e*) can be distinguished which marks the position of the embryo, the remaining yellow part of the contents of the grain consisting of endosperm. At that end of the oval depression which lies remote from the scar of attachment of the grain, careful examination will reveal a second scar-like projection, the remains of the stigma (*st*). This shows us that the grain of the Maize (also that of the other Grasses mentioned above) is still enclosed in the ovary-wall and therefore really represents a fruit containing a single seed. As a matter of fact, in the Grasses the

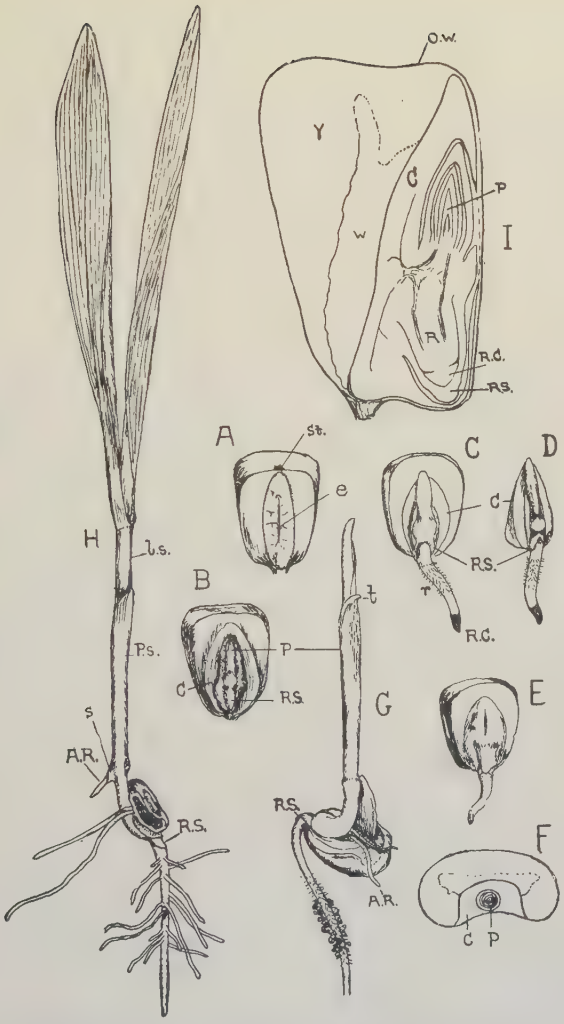


FIG. 18.—Structure of grain and germination in the Maize (all figures slightly enlarged, I ×8). A, Entire grain showing outline of embryo. B, Grain with envelope removed and edges of cotyledon folded back to show plumule and radicle. C, Early stage in germination, envelope removed. D, Embryo of same, dissected out. E, First stage in germination. F, Cross-section of grain with envelope removed. G, Late stage in germination showing escape of foliage-leaves from sheath. H, Mature seedling. I, Longitudinal section of complete grain (much enlarged). *A.R.*, adventitious (secondary) roots; *c*, cotyledon; *e*, embryo; *l.s.*, leaf-sheath; *O.W.*, ovary-wall; *P*, plumule; *P.s.*, plumular sheath; *R*, radicle; *R.C.*, root-cap; *R.S.*, root-sheath; *S*, sheath round base of secondary roots; *st*, stigma; *t*, tip of plumular sheath; *W*, starchy endosperm; *Y*, sugary endosperm.

seed-coat is joined up with the surrounding ovary-wall (cf. p. 278), so that the two cannot be readily distinguished from one another, and as a consequence the micropyle cannot be seen. A little above the middle of the white patch caused by the embryo, at the end nearest the stigma-scar, a shallow and slightly darker depression, which marks the position of the plumule, is frequently recognisable.

If the envelope is carefully removed from a soaked grain of Maize, the white embryo and the yellow endosperm are readily distinguished. A somewhat darker line runs vertically up the face of the exposed embryo. By cutting a shallow slit along this line with the extreme point of a penknife and turning back the two edges of the cotyledon thus obtained (Fig. 18 B), two peg-like projections are exposed, one directed towards the original point of attachment of the grain and representing the radicle (*R.S.*), the other placed in the opposite direction and constituting the plumule (*P*). The remainder of the white embryo comprises the single large cotyledon (*c*) which, as we have seen, is wrapped round both plumule and radicle (cf. below).

A further insight into the structure of the embryo is obtained by halving the peeled grain lengthwise along the same dark line as before (Fig. 18 I). The embryo is then seen to occupy the whole of the base of the seed, but tapers off to one side above, whilst the cotyledon (*c*) lies in close contact with the endosperm. The short blunt radicle (*R*) (terminated by a darker root-cap, *R.C.*) is now easily recognised and is seen to be enclosed in a special cap-like sheath, the *root-sheath* (*R.S.*, also seen in Fig. 18 B), whilst the plumule (*P*) consists of the central growing point encased in a succession of sheathing leaves (see also *P* in Fig. 18 F, which represents a cross-section of the grain at the level of the plumule). From one side of the axis of the embryo, at the point where plumule and radicle join, the large shield-shaped cotyledon (*c*) arises on a short thick stalk. The whole margin of the cotyledon is drawn out, so as to surround the rest of the embryo (see Fig. 18 F), leaving a slit-like aperture opposite the plumule. Careful examination with a lens shows that the root-sheath and the outermost sheath of the plumule both arise near the point of attachment of the cotyledon.

It will have been noticed that the soaked grains of Maize exhibit a slight increase in size as compared with the dry ones.

Around the former point of attachment of the grain is some whitish chaff (representing remains of the Maize flower) which probably facilitates the absorption of water at this point. As a result the radicle is again the first part of the embryo to receive water and the first to emerge, bursting through the skin of the grain and growing down into the soil (Fig. 18 E) ; around its base the split root-sheath can be plainly distinguished (*R.S.* in Fig. 18 C and D). The appearance of the radicle is very soon followed by the outgrowth of the plumule, which in this case pierces the skin by its *own active growth* and pushes its way to the surface (Fig. 18 C and D). It will be found that the radicle does not grow into a sturdy main root as in the Bean or Castor Oil, but is almost immediately followed by a number of similar roots (Fig. 18 G, *A.R.*), developing from within the seed near the base of the radicle and sometimes recognisable already before germination ; these secondary roots often grow more vigorously than the primary one which is soon indistinguishable from them.

The plumule, unlike that of the Dicotyledonous seedlings, remains straight during its passage through the soil, but the tender growing point and the young leaves encasing it are nevertheless amply protected by the outermost sheath, the tip of which (*t* in Fig. 18 G) is hard and pointed. It is thus again not the tender plumule that has to endure friction with the particles of the soil, but a structure (viz. the tip of the outermost sheath) already matured within the seed. Soon after the surface of the ground is reached, the inner leaves of the plumule begin to grow rapidly and bursting the outermost sheath become exposed to the light (Fig. 18 G and H). In these foliage-leaves we can distinguish two parts, the narrow green blade and a paler portion (the leaf-sheath) which fits closely around the stem (Fig. 18 H, *l.s.*). The outermost envelope of the young plumule, having served to protect it whilst piercing the soil, remains as a sheath around the base of the stem (Fig. 18 H, *P.s.*), differing only from the later leaves in the absence of a blade which would only have impeded its progress.

During the whole process of germination the cotyledon remains underground within the seed and is actively absorbing nourishment for the growing embryo from the adjacent endosperm. When examining the grain it will have been noticed

that two regions are distinguishable in the latter, the portion nearest the embryo being white and relatively soft, whilst the remainder is yellow and harder (Fig. 18 I, *W* and *Y*). If we halve a grain lengthwise and treat the cut surface with Iodine, it will be found that the white portion alone gives the starch-reaction, the remainder of the endosperm chiefly containing sugar. The outlines of the cells (cf. p. 7) constituting the endosperm can, with the help of a lens, be seen as a polygonal network, within the meshes of which the coloured groups of starch are situated. As in the case of the Castor Oil seed, the reserve food-material of the endosperm will be found to have appreciably diminished in grains attached to older seedlings.

The Onion will serve as a second example of a Monocotyledonous seed. In the dry condition this is a more or less wrinkled structure, with three irregular faces and provided with a black testa (Fig. 19 A), one of the edges being prominently concave. If a number of seeds are cut lengthwise, so that the plane of section passes through the concave edge and the opposite face, a structure similar to that shown in Fig. 19 B will be found in one or the other case. It will be seen that, apart from the testa, the seed consists of a mass of greyish-white endosperm (*e*) containing near the margin a whitish coiled embryo ; the latter appears to be a uniform structure, but in fact consists of a radicle (*R*), grading over imperceptibly into the cotyledon (*c*) which completely ensheathes the plumule.

Owing to the hard testa there is no appreciable increase in size when the seed begins to take up water. The first evidence of germination (Fig. 19 C) is as usual the appearance of the radicle (*R*) at one end of the seed, and this is followed by elongation of the embryo as a whole (Fig. 19 D). The green colouration which is rapidly assumed by the part nearest the seed now enables us to distinguish the cotyledon (*c*), the tip of which remains embedded within the endosperm, from the white radicle (*R*) which is becoming firmly established in the soil. In the course of its further elongation the cotyledon becomes prominently arched, this arch being retained for a considerable period, and by its continued growth in the upward direction the seed is often raised considerably above the surface of the ground (Fig. 19 E). At this stage the base of the cotyledon exhibits a slight swelling owing to increase in size of the contained

plumule, whilst secondary roots frequently develop just below this level (Fig. 19 E, *a.r.*). Finally the plumule bursts through

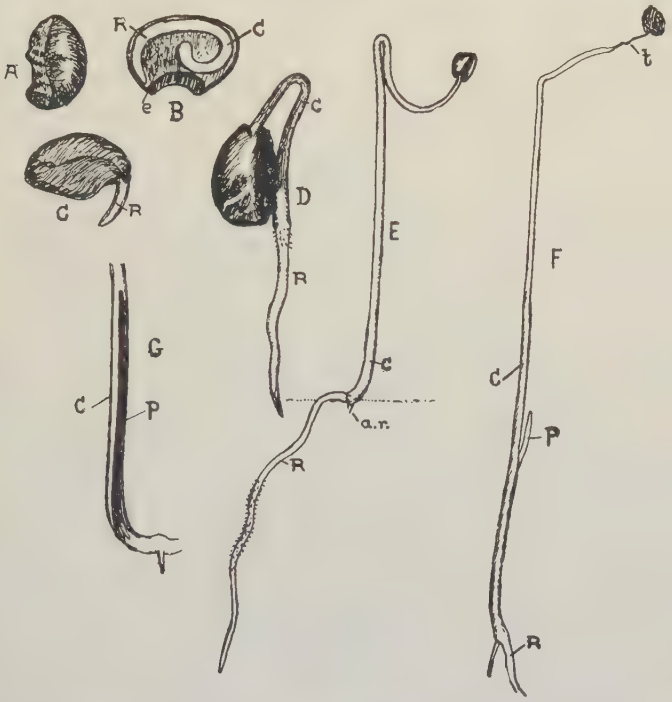


FIG. 19.—Structure of seed and early stages of germination of the Onion (A–D and G considerably enlarged, E and F about twice natural size). A, Entire seed. B, Seed halved lengthwise to show embryo and endosperm. C, Emergence of radicle. D, Elongation of cotyledon. E, Older seedling showing swelling at base of cotyledon due to plumule. F, Appearance of plumule and withering of cotyledonary tip. G, Longitudinal section of base of cotyledon in stage E, to show contained plumule. *a.r.*, adventitious root; *c*, cotyledon; *e*, endosperm; *P*, plumule; *R*, radicle;

the cotyledonary sheath (Fig. 19 F) and commences to unfold its leaves.

We see that throughout germination the tip of the cotyledon remains within the seed serving to transfer the food-materials

from the endosperm to the growing plant. In late stages, such as that seen in Fig. 19 F, the seed will be found to be almost empty and, on cutting it in half, shows apart from the withered tip of the cotyledon only shrivelled remnants of the endosperm. The cotyledon functions then in the same way as that of the Maize, but whereas in the latter the entire structure is employed for purposes of absorption, in the Onion the larger part emerges

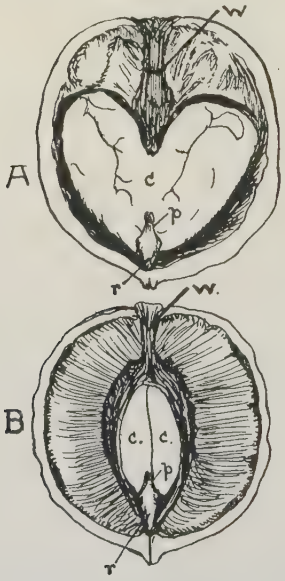


FIG. 20.—Structure of the Walnut (natural size). A, Section cut lengthwise *between* the two halves of the shell. B, Section cut lengthwise at right angles to the plane of A. *c*, cotyledon; *p*, plumule; *r*, radicle; *W*, wick-like strand.

from the seed, becomes green and not only serves as an assimilatory organ, but also constitutes the means of liberation of the plumule. It will thus be recognised that the Onion exhibits a fourth type of germination differing from the three hitherto considered. The germination of the Date is similar in all essentials, but takes place so slowly as to be less suitable for purposes of study.

Having become acquainted with these few types we may

now consider certain aspects of germination. We have seen that water is a prime necessity and that, in order to facilitate its absorption, many seeds are provided with definite mechanisms (*e.g.* the pocket of the Bean, the caruncle of the Castor Oil, etc.). A still more striking example is furnished by the Walnut (Fig. 20) which, when halved longitudinally, shows a prominent wick-like strand (*W*), running from one end of the nut to near its centre and terminating some little distance from the tip of the plumule (*p*). The water diffuses through this strand and from it passes into the thin membranous plates lying between the lobes of the cotyledons (*c*), thus reaching not only the latter, but also the tip of the radicle (*r*), as can be easily seen in fresh Walnuts which have been immersed for some hours in red ink. In other cases the whole seed-coat readily takes up water owing to its slimy character, which is well shown by the Cress, Mustard, and Clary. A number of seeds again have marked corrugations or pittings of the surface of the testa (*e.g.* Corn-cockle, Primrose) in which, after wetting, water is readily retained.

The immediate effect of this absorption of water is invariably the escape of the radicle, and in many cases its penetration into the soil is aided by devices for fixing the seeds (*e.g.* the slimy seed-coats already mentioned in the last paragraph). The culmination of the process of germination is the liberation of the plumule, and we have so far learnt that this may be effected in four different ways, viz. by elongation of the stalks of the cotyledons (Bean), by elongation of the hypocotyl (Castor Oil), by its own direct growth (Grasses), and by growth of the cotyledon (Onion). In the majority of seeds the plumule is liberated according to one of these four methods, but as a somewhat exceptional case we may instance the Vegetable Marrow. The flat exalbuminous seeds of this plant germinate on the surface without means of fixation, but a special peg-like outgrowth develops from the base of the hypocotyl which not only forces apart the two halves of the seed-coat, but serves to keep the lower firmly pressed onto the soil. The subsequent liberation of the plumule (and cotyledons) takes place as in the Sunflower (Fig. 17).

In the previous descriptions attention has been drawn to the fact that the young plumule is always protected in some way or other during its passage through the soil, *e.g.* by its own

curvature in the Bean, by the outermost leaf-sheath in the Maize, etc. The straightening of the plumule in the first case and the bursting through of the enclosed leaves in the second result from exposure to the light on emergence from the soil. Seedlings of either type grown in darkness show no such change, and an instructive experiment can be performed in this connection. We may employ for this purpose a rectangular wooden box which is perforated by a number of small holes to allow of drainage, one long side being replaced by a sheet of glass (Appendix III.) sloping inwards from the base at a slight

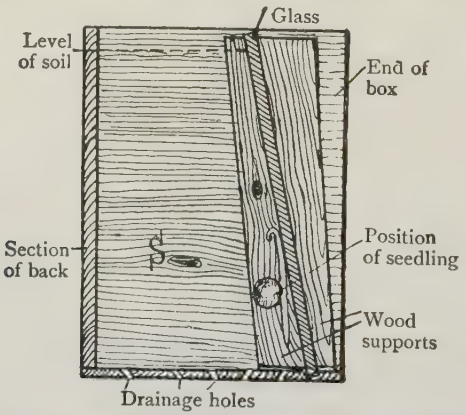


FIG. 21.—Diagram of section of box to be used in experiment described on p. 44, showing method of fixing sloping glass front, the position of the seedlings, and the soil (*s*).

angle (cf. the section in Fig. 21). A thin layer of moist earth is placed on the bottom and seeds are sown in this in close contact with the glass, after which the box is filled with soil. The right or left hand half of the glass is covered with black paper, whilst the other remains exposed to the light.

The seeds which develop in darkness germinate in the normal way and sooner or later their plumules appear above the surface (Fig. 22 B). Owing to the inward slope of the glass the plumules remain in contact with it, so that those of the seeds germinating behind the uncovered portion are exposed to the light from the outset, though still beneath the soil. As a result the plumule straightens out or, in the case of the Maize, bursts through

the protecting sheath prematurely. The plumules under these circumstances are so unsuited to force their way through the soil, that they not only fail to reach the surface, but become more or less zigzagged (Fig. 22 A) in their attempts to do so. This experiment demonstrates that the altered behaviour of the plumule after emergence from the soil is due to illumination, and that without the usual protective devices it would fail to reach the surface. The shoots of many herbaceous perennials

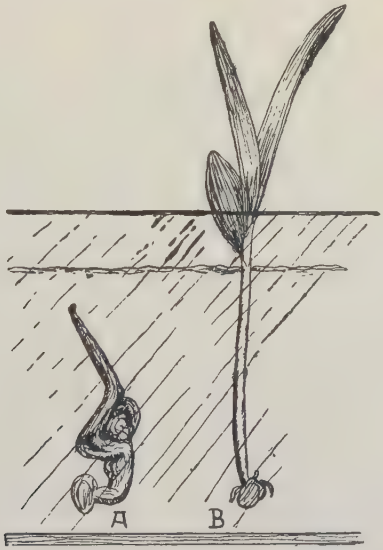


FIG. 22.—Two Maize seedlings. A, Grown exposed to light from beginning of germination. B, Grown in darkness till surface of soil is reached. (Reduced to two-thirds natural size.) See text.

with underground stems show a similar curvature of their tips during their passage through the soil (*e.g.* Dog's-mercury, Moschatel, Wood Anemone, etc.).

Cotyledons either serve directly as storage-organs or as a means of transference of the food-material from the endosperm. In either case they may shrivel up after these purposes are fulfilled, or they may subsequently appear above the ground and function for a time as organs of assimilation. Such epigeal cotyledons are always simple in form and among

Dicotyledonous plants usually differ to a more or less marked extent from the subsequent foliage-leaves, as will be quite apparent from a consultation of Fig. 23. In many cases the leaves immediately following on the cotyledons have a simpler form than those developed later, and this is especially marked in plants whose mature leaves are deeply divided (*e.g.* the Greater Celandine, Fig. 23 B).[1] The foliage in such cases exhibits a progressive increase in complexity as the plant

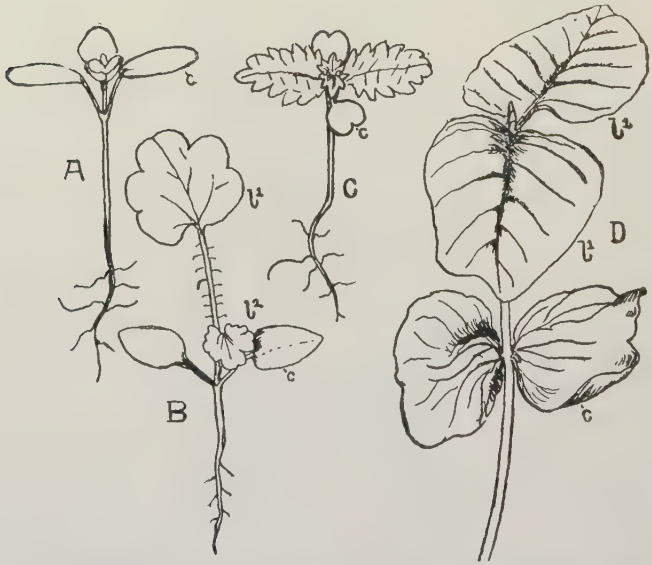


FIG. 23.—Different types of Dicotyledonous seedlings (all natural size). A, Garden Spurge. B, Greater Celandine. C, Stinging Nettle. D, Beech. *c*, cotyledons ; l^1 and l^2, first and second foliage-leaves.

grows older, and a similar transition can often be observed on the shoots of herbaceous perennials, *e.g.* the Musk-mallow (Fig. 24) and the Sheep's Scabious. Further excellent examples are afforded by the young Fern plants, always to be found growing in conservatories. Another peculiarity often shown by the first pair of leaves lies in their tendency to arise together from the same node, even when those developed later occur

[1] For other examples of transition in seedlings, see p. 178 and p. 216.

singly (*e.g.* in the Beech, Fig. 23 D, and the Runner Bean, Fig. 13 C).

Even in the mature plant the leaves at the base of a branch not infrequently differ from those produced later. Thus, in

FIG. 24.—Transition of foliage in the Musk-mallow (about half the natural size). A, Radical leaf. B–D, Cauline leaves borne at progressively higher levels on the shoot.

the Pelargonium the first two leaves of each branch arise from the same node, whilst the later ones occur singly; in the Willow the two scales enveloping each bud are the first two leaves of the shoot to which the latter gives rise.

CHAPTER V

The Root and its Functions

We have seen in the first chapter that the two chief functions of the root are attachment to the soil and absorption of water, and we may now obtain a further insight into the suitability of the root for these purposes. If the root of a young Bean- or Pea-seedling (Fig. 25) is examined, we can distinguish, as in the Shepherd's-purse, root-cap (*r.c.*), root-hairs (*r.h.*) and

Fig. 25.—Young Pea-seedling with radicle showing root-hairs (*r.h.*) and root-cap (*r.c.*), after being kept in water (about twice natural size).

lateral roots (cf. Fig. 14 of the Bean). The two former are again best seen, if the seedlings have been kept for two or three days in water.

The root-cap serves the purpose of protecting the delicate cells of the growing point at the tip of the root from injury whilst the latter is forcing a passage through the soil. During the elongation of the root the outer surface of the cap gradually breaks down and becomes slimy, so that the root-tip glides

easily between the particles of earth. As the substance of the root-cap wears away in front, new tissue is continually formed from the growing point behind and thus the cap remains of almost constant thickness.

It will be noticed that there is a varying extent of bare root between the apex and the region occupied by the root-hairs (Fig. 25). It is in this region, and here only, that increase in length is taking place in the new units (cells) formed by division of the cells of the growing point (p. 7). To demonstrate this fact we take a number of seedlings having straight radicles (see Appendix IV.) about an inch long and, using Indian ink, mark off horizontal lines (see Appendix V.) along the root, at intervals of one millimetre from the apex backwards

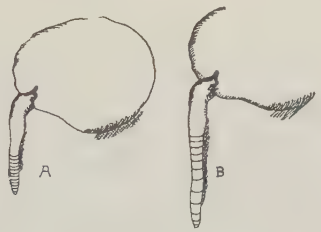


FIG. 26.—Experiment to demonstrate region of growth in radicle of Broad Bean (about half the natural size). A, At the beginning of the experiment. B, Forty-eight hours later.

(Fig. 26 A). The seedlings are then attached to a piece of cork by pins passing through the cotyledons and fixed with the roots pointing vertically downwards in the neck of a jam-jar, the sides of which are lined with wet blotting-paper. The whole should then be put in a warm dark place for about forty-eight hours. If the roots be now examined, it will be found that the marks are no longer at equal intervals, but that some have separated more or less appreciably, whilst others have practically remained at the original distance of one millimetre (Fig. 26 B). Little elongation has taken place, for example, between the lines at the extreme tip, or between those on the part of the root adjacent to the seed. On the other hand, the distance between the fourth and fifth marks has increased very considerably, while the intervals above

and below will be found to have elongated to a less and less extent until we reach the regions at base and apex where, as we have seen, no alteration has taken place.

It is thus apparent that growth in length of the root takes place in a very restricted zone, situated a little way behind the apex. It will also be gathered that growth involves two distinct processes, viz. the actual division of the cells of the growing point resulting in the formation of new units,

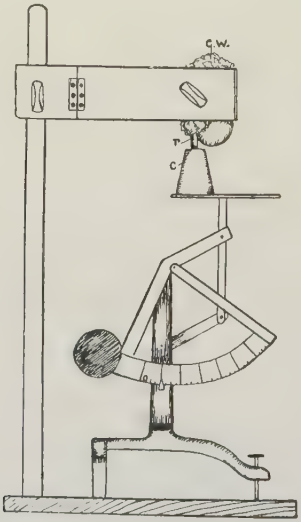


FIG. 27.—Experiment to demonstrate the force exerted by roots in their downward growth. For description, see text. *c*, cork ; *c.w.*, cotton-wool ; *r*, radicle.

and the subsequent enlargement of these, mainly in the longitudinal direction, until they have reached their adult dimensions.

It is obvious that, in order to pierce its way through the soil, the growing root must be capable of exerting considerable force, some idea of which can be gained from the following experiment (Fig. 27): To the centre of the platform of an ordinary letter-balance a one-inch cork is firmly fixed with sealing-wax or glue, the upper surface of the cork being scooped out so as to create a hollow about half an inch deep and a

quarter of an inch across (this should be lined with soaked cotton-wool). A Bean-seedling having a straight radicle (see Appendix IV.) about three-quarters of an inch long is arranged, as shown in Fig. 27, so that the root-tip fits vertically into the hollow of the cork. The seed is best covered with soaked cotton-wool in order to keep the radicle supplied with water, whilst any space between the root-tip and the sides of the hollow in the cork can be packed with the same material. As the root grows, the platform of the balance becomes more and more depressed, and to effect this it is plain that a certain amount of force must be exerted.

This force is a result of the increase in size of the cells in the zone of elongation and in nature; where the older part of the root is firmly fixed by root-hairs and lateral roots, it serves to drive the apex downwards. Moreover, owing to the restriction of growth in length to a short region, the driving power is exerted close to the apex and therefore the direction of application of the force and the moving tip tend to remain in the same straight line; thus a maximum effect is secured. The growing part of the root is comparable to a short nail driven into a piece of wood. On the other hand, a long slender nail, in which the driving force is applied some distance from the point, is very liable to become bent, and the same statement would apply to a root in which the zone of elongation was situated some way from the tip.

We have already noticed that the root-hairs arise above the elongating portion of the root, and the advantage of this is clear when we remember that their purpose is to absorb water from the soil (p. 8), a function which could not be fulfilled if their position were continually altering with the growth of the root. Moreover, under such conditions the delicate root-hairs would become torn and useless. As it is, however, they always develop from that part of the root which has just concluded its growth in length. The root-hairs, which are narrow tube-like outgrowths of the surface-cells (Fig. 58, p. 107), insinuate themselves between the small particles of the soil (Fig. 33, p. 62), with many of which they come into very close contact. It is owing to this that even after careful washing beneath a tap of running water small soil-particles still cling to the finer branches of the roots of most plants.

It is, however, not only the front part of the root that is devoid of root-hairs, for it is seen that the latter occupy a relatively short zone and that the hinder part is again bare (Fig. 25). This is because the root-hairs are transient structures lasting only a few days, new hairs sprouting out in front as the older ones die away behind. The new hairs arise from surface-cells in which elongation has just ceased and thus, whilst the part occupied by root-hairs always remains at the same distance from the root-apex, the hairs follow the growing tip as it penetrates through the soil. Since root-hairs are

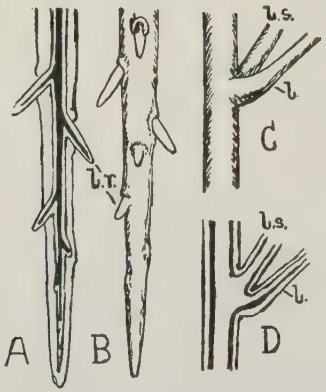


FIG. 28.—Diagram to explain the origin of lateral roots and shoots. A, Longitudinal section of root. B, Exterior view of same. *l.r.*, lateral root. C, Exterior of node of stem. D, Longitudinal section of same. *l*, leaf; *l.s.*, lateral shoot.

developed in exactly the same way on the lateral roots, the growth of the whole root-system carries the region of absorption into new areas of the soil.

The side-roots will be found to arise at some considerable distance from the tip of the main root (Fig. 13 C, Fig. 15 E), and careful observation shows that they have burst through the outer covering of the latter (Fig. 28 B). If we now cut the main root lengthwise into two equal halves with a sharp pocket-knife, it will be seen (Fig. 28 A) that the branch-roots arise from the central core of hard substance with which we have already become familiar in the Shepherd's-purse (p. 2)

and which is a feature of all roots. A short distance behind the apex young laterals, which have not yet reached the surface, are distinguishable (Fig. 28 A), whilst farther back others are seen piercing through to the exterior. The laterals thus originate in the interior of the parent-root, and the branching of the root is therefore described as *endogenous*. In this way the young branch is nurtured within the mother-root, until it is fully equipped to make its own way through the soil. It is further of utility that the laterals should not emerge from the portion of the root undergoing elongation or bearing root-hairs. It will be noticed that the side-roots do not arise indiscriminately from the main root, but that they form a number of vertical rows, generally four or five (Fig. 28 B, Fig. 16 A, p. 33).

We have thus come to recognise the following regions in the main root: the root-cap, the growing point, the zone of elongation, the zone of root-hairs and the mature zone bearing laterals. All, even the finest members of the root-system, show an identical structure, and the principal difference between the main root and its branches lies in their direction of growth. We have frequently had occasion to remark that the main root grows vertically downwards into the ground, and we will now enquire as to the reason. To solve this problem the following experiment may be performed.

A number of healthy seedlings having straight radicles (see Appendix IV.) are pinned parallel to one another to the surface of a large cork; the latter is then fixed edge on by means of a nail to the bottom of a large light-tight box in such a way that the radicles are horizontal and free to bend. The entire inner surface of the box (including the lid) is lined with wet blotting-paper, and the whole is then left in a warm place for about twenty-four hours. If the radicles are then examined, the tips will be found to have curved downwards into a vertical position. It is plain that the roots were subjected equally on all sides to moisture, warmth, supply of air and darkness, and the only one-sided influence lay in the force of gravity acting towards the centre of the earth. The root then, unlike the shoot of most plants (cf. p. 18), grows in the direction of this force and is thus led to penetrate deeper and deeper into the soil. On the other hand, light which, as we have seen, plays

an important part in determining the direction of growth of the shoot, has little influence on the roots of most plants.

Examination of the root-system of such plants as the Shepherd's-purse and the Pea at once discloses the fact that the laterals diverge at more or less of an acute angle from the main root, so that they grow outwards and downwards (Figs. 2, 13, 15). In order to observe readily the growth of the root-system we can employ a rectangular wooden box, provided with drainage-holes as described on p. 44 ; one long side of the box is again removed and replaced by a sheet of glass (see Appendix III.) which in this case, however, slopes *inwards* from the top at a slight angle. The box is then filled with soil and seeds are planted in the top of the latter in close contact with the glass, the whole being placed in darkness. Owing to the downward tendency of the root-system the main root and its laterals, as they develop, remain in close touch with the glass surface. We now prop up one end of the box so that its floor is at an angle of 45° with the ground, and leave the experiment for about three days. It is then observed that the tip of the main root, as in the preceding experiment, has curved down into the vertical position ; the tips of the laterals have also curved, so that these tips now lie at the same angle as before with the new direction assumed by the growing part of the main root—a fact which can be verified by measuring the old and new angles with a protractor. We thus see that the direction of growth of the laterals is also influenced by gravity, but bears a constant relation to that of the main root.

Arising from the laterals of the first order, which we have just considered, are smaller roots of the second order, and in a strongly developed root-system there may even be branches of a higher order (Fig. 2). These ultimate members of the root are unaffected by gravity and generally extend into the soil in all directions. Hence the volume of soil occupied by the root-system is very completely exploited by its numerous ramifications.

Apart from gravity, there is, however, one other condition that markedly influences the direction of growth, especially of the finer branches of the root-system, and that is the distribution of moisture. To demonstrate this fact we use the same box as in the last experiment with the following modifica-

tion (Fig. 29): A small clean flower-pot, the hole at the base of which is firmly plugged to prevent leakage, is filled with water and embedded up to its rim in the soil which otherwise fills the box and which should be moderately dry. Soaked seeds (*e.g.* Pea, Bean) are planted against the glass as before, but some are also placed in the surface-layer of the soil in other parts of the box. Water is supplied to the soil only by way of the flower-pot which is kept full. After having remained in darkness[1] for about ten days, the roots of the seedlings planted against the glass are scarcely visible and, on uprooting them

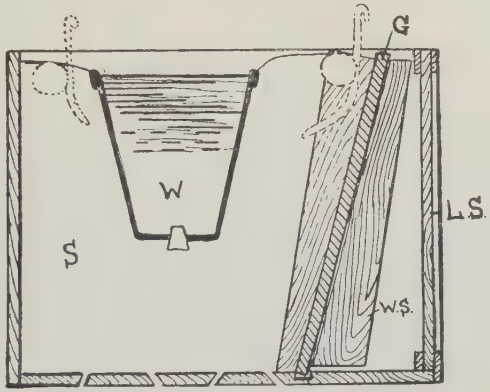


FIG. 29.—Experiment to demonstrate hydrotropism in roots. The box is shown in section; the final appearance of two seedlings is indicated by dotted lines. *S*, soil; *W*, water in central pot; *G*, sloping glass front of box; *L.S.*, light-shield. *W.S.*, wooden supports for glass front.

carefully, it will be seen that this is due to their having curved more or less markedly towards the pot which is the only source of moisture in the soil (see Fig. 29). Moreover, the seedlings which have developed from the seeds planted elsewhere in the box will, if carefully pulled up, also show a marked curvature of their roots towards the pot. This influence of one-sided moisture on the direction of growth of roots is described as *hydrotropism*.

The type of root-system with which we have hitherto become familiar (*e.g.* in the Shepherd's-purse, Fig. 2; the Pea,

[1] This can be effected by means of a wooden light-shield, shown in Fig. 29.

Bean, etc., Fig. 13) is characterised by the possession of a prominent main root (often spoken of as a *tap-root*) growing vertically down into the soil and bearing numerous branches that become progressively smaller. This type is most commonly found in Dicotyledons. In Monocotyledons, on the other

FIG. 30.—Different types of root-systems (reduced to about half natural size). A, Carrot. B, Lesser Celandine. C, Grass. D, Turnip. The level of the ground is in all cases shown by a black line. *l*, leaf-scar.

hand, as well as in many Dicotyledons, the root-system consists of a number of members in which we cannot distinguish any single one as specially prominent; such a root-system is described as *fibrous*, and good examples are furnished by the Strawberry (Fig. 85, p. 154), the Hyacinth and Grasses (Fig. 30C). As a matter of fact we have already met with an instance of this kind in considering the germination of the Maize (p. 39).

In all fibrous root-systems the radicle, which in the first type mentioned gives rise to the tap-root, fails to develop tc any considerable extent. The tuft of roots originates either by outgrowth from the base of the stem (as in Grasses, Strawberry, etc.) or from the hypocotyl (as in the Groundsel and Sanicle). In such cases, owing to the fact that they do not arise from a like organ, the roots are described as *adventitious*. Another good example of such adventitious roots is seen in the Ivy (Fig. 31), where they appear on the side of the stem adjacent to the wall and serve to fix the plant. The propagation of plants by cuttings (*e.g.* Geraniums, Osier-willows) is dependent upon the development of adventitious roots from the part of the stem placed in the soil. In many Willows the

FIG. 31.—Portion of a climbing shoot of Ivy, showing the adventitious roots and three nodes (somewhat reduced).

rudiments of these roots are visible as little knob-like swellings beneath the nodes.

In plants in which the overground organs persist and form a woody skeleton, as we see it in shrubs and trees, the development of this aerial system is accompanied by a similar change in the root. Most trees at first possess a tap-root, but as the plant becomes older we find that the laterals near the surface of the soil frequently develop more strongly and form a horizontal platform which serves to support the plant and distributes the pulling strain (due to the action of the wind) over a wider area. Such roots often appear above the surface of the ground as a system radiating from the base of the main trunk, this being due to their own increase in thickness, as well as to removal of soil by rain. The bulk of such a woody root-system no longer serves the purpose of absorption, this function being restricted to its finest branches. It is a familiar fact

that the foliage of most trees affords a more or less efficient shelter from rain, the water draining off from the edge of the canopy. Since the roots develop *pari passu* with the crown of foliage, their absorbent branches are thus usually located beneath the drip of the tree.

An interesting example of a special development of the root-

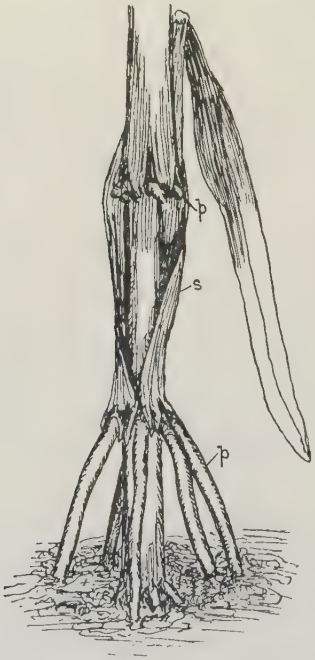


FIG. 32.—Lower part of plant of Maize, showing prop-roots (*p*) arising from two nodes, the upper ones in an early stage of development (about natural size). *s*, sheath of lowest leaf.

system is found in the Maize, in which after the plant has reached a certain height additional adventitious roots arise from the stem, some little way above the surface of the ground, and grow obliquely downwards into the soil (Fig. 32). These *prop-roots* serve the purpose of augmenting the somewhat feeble primary root-system which is insufficient to maintain the tall Maize plant in the erect position. Better examples are

furnished by the tropical Mangroves which grow in loose shifting estuarine mud subjected to tidal inundation.

In biennials and herbaceous perennials the roots frequently serve as storage-organs for the food-materials, laid up for subsequent growth (see Chapter II.), and in consequence become more or less swollen. Frequently it is the tap-root which enlarges in this way, and good examples are furnished by the Carrot (Fig. 30 A), the Parsnip, the Salsify, the Dandelion and the Dock. In the Dahlia and Lesser Celandine (Fig. 30 B), on the other hand, we have a fibrous root-system, many of the members of which are swollen, and in such a case the enlarged roots are often spoken of as *root-tubers*. The swollen structure in the Turnip (Fig. 30 D) consists largely of a tap-root, but in the formation of the uppermost portion the hypocotyl and the base of the stem appear to participate, since remains of leaves are often found in this region (Fig. 30 D, *l*). The underground tubers of British Orchids are swollen roots bearing a bud at their apex. The examples just given include a number of our common vegetables which owe their utility to the large quantities of food-reserves contained in the storage-organs concerned, and as further instances we may add the Radish, the Beetroot and the Mangold-wurzel.

CHAPTER VI

The Soil

The soil from which the roots of plants derive so important a part of their nourishment is a more or less loose aggregation of two kinds of particles. On the one hand we have the mineral particles formed by the breaking down of rocks under the influence of atmospheric and other agencies; on the other hand we have the organic particles consisting of the decayed remains of plants and animals that have previously lived on the soil in question, such organic material being spoken of collectively as *humus*.

The mineral particles, which usually exceed the organic in amount, will depend in their nature on the kind of rock from which they have been derived. Thus, the soil in a sandstone or gravel area will tend to consist in the main of so-called sandy particles, *i.e.* of relatively large grains of semi-transparent quartz which are, however, frequently coloured red or brown by iron-compounds. Similarly, in a chalk area we find a considerable proportion of chalk particles in the soil (calcareous soil), which in consequence is often conspicuous by its greyish-white colour. A soil of a more mixed character is found in those regions where the rocks are of volcanic origin (igneous rocks, *e.g.* granite, basalt, etc.), since such rocks are composed of many different kinds of minerals (*e.g.* quartz, felspar, mica and hornblende, the commonest constituents of granites).

In all the cases just mentioned we are dealing with soils formed *in situ*, and there is thus, apart from such chemical changes as may have taken place, a close relation between the character of the soil and the nature of the underlying rock. But this need not necessarily be the case. The material formed by the breaking down of rocks may be carried away by running water which, according to its rate of flow, has the power of

transporting particles of varying size, and the latter are thus deposited at some distant point when the current decreases in rapidity. In this way there arise the large stretches of alluvial soil, generally clayey in character, so commonly found near the mouths of rivers. Movement of glaciers in the past (during the glacial period) has also been instrumental in the transference of surface-soil, for by the disintegration of the boulders, etc., transported upon the ice, large areas of clay and gravel have been produced (*e.g.* Hertfordshire Boulder clay, glacial drifts of Norfolk).

As a general rule the soils one meets with in nature are mixed soils in which, however, one kind of particle often predominates, pure soils being relatively rare. In order to obtain some insight into the structure of a soil we may proceed in the following way: One or two lumps of *unbroken* earth are first placed in a vessel of water and moved about to displace the air from their surfaces; if they now be broken up, bubbles will be found to arise from them showing the presence of air within the soil. The amount of this air can be estimated in the following way.

A tin which must not leak is filled to the brim with water and completely immersed in a tall glass cylinder partly filled with the same liquid; the level of the water in the cylinder is then marked by a piece of gummed paper. The tin, still full, is next removed and after the moisture from its surface has been allowed to drip into the cylinder, it is emptied and a number of holes punched in its base. Thereupon the open end is driven down into the soil *in situ*, until the tin is completely filled, after which it is dug out and the soil in the tin cut off flush with the edge. The whole is now placed in the cylinder and the contained soil is scooped out under the surface of the water, so as to ensure complete displacement of the air. The water in the cylinder is then seen to stand at a lower level than that previously marked by the piece of gummed paper. By adding water from a measuring-glass until the marked level is reached, we obtain a moderately exact estimate of the amount of air in the volume of soil used.

There must thus be a more or less considerable number of spaces in the soil which are occupied by air (Fig. 33, *a*). The latter stands in connection with that of the atmosphere and is continually circulating from one part of the soil to another,

being of immense importance in the respiration of roots and of the organisms (*e.g.* Bacteria, Protozoa), which live near the surface. Whenever soil is dug up or otherwise worked, the amount of air in the interspaces increases, so that such soil occupies a larger volume than before. A correct estimation of the natural air-content can therefore only be obtained, if the method described in the last paragraph is adopted.

Since a considerable space in the soil is occupied by air, the question arises as to where the water is situated. If a small

FIG. 33.—Diagram of soil with root-hairs (*r.h.*) to show the distribution of air (*a*) and water (*w*) (much enlarged). The soil-particles are shown black, the water-films are stratified.

quantity of moist earth is spread out in a thin layer on a sheet of white paper, the individual particles will be seen to have a fresh or glistening surface. The paper with the soil may now be placed in the hot sun or near a stove for some hours and again examined, whereupon the particles will be found to appear dull. The glistening was due to a very thin film of water which coated each soil-particle and was removed by evaporation in the second case. In a soil which is capable of supporting a healthy growth of plants, the moisture occurs mainly as such films (Fig. 33, *w*), which coalesce so as to fill

the smaller interspaces, but surround the air in the larger ones. Most bodies after immersion in water show a similar film which is due to an adhesive force operating between the water and the surface of the body.

If it be desired to determine the *water-content* of the soil, 100 grams are placed in a weighed evaporating dish, after which dish and soil are heated over a water-bath (Appendix VI.) for several hours at a temperature slightly below 100° C. After cooling, the whole is reweighed and we thus obtain the weight of the soil less that of its water. It is, however, necessary to heat again and reweigh until two successive estimations afford the same result ; only then has all the water been driven off. Subtracting the weight of the dish, the difference between the first and the final weight represents the water-content in 100 grams of the soil, the result being usually expressed in percentages of the original amount.

We now know how much air and how much water our soil contains and where these are situated, and we may next subject a sample to a rough *mechanical analysis*. For this purpose a small quantity is placed in a tall glass cylinder which is then nearly filled with water. Thereupon the contents are thoroughly stirred with a stick until the liquid is uniformly turbid, after which the soil is allowed to settle. Very soon the coarser sandy particles begin to collect at the bottom, and these are quickly followed by others of progressively smaller size till finally (after many hours or days) the clayey silt becomes deposited as the uppermost layer, leaving the water clear. In this way a very rough separation of the soil into particles of diverse sizes is obtained, and the approximate amount of each can be determined by measuring the thickness of each layer. The relative quantities of fine and coarse particles will, however, be found to vary considerably in different types of soil.

At the end of the previous experiment there is still a portion of the soil floating at the surface of the water. This consists of dark-looking fragments, the vegetable nature of which can often be recognised, and these constitute the organic material or *humus* (cf. p. 60). The amount of the latter can be readily determined by strongly heating a weighed portion of the *dried* soil in a crucible over a Bunsen burner for some hours. When cool the soil is reweighed, after which it is again heated until

two consecutive weighings afford the same result. The difference between the original and the final weight gives the humus-content.

A number of soils from various localities should be examined in the above manner, when it will be found that they not only differ widely from one another as regards their air-, water- and humus-contents, but also as to the relative proportions of coarse and fine particles. At the two extremes we should have sandy gravels with practically nothing but coarse particles (*e.g.* a pebble-beach), and clayey soils and silts composed almost wholly of fine particles; the London basin furnishes good examples of clayey soils, whilst silts are largely alluvial and best seen near estuaries. But between the two extremes there are many intermediate types. Thus, soils consisting of sandy and clayey particles in practically equal amount are known as *loams*, those in which the coarser predominate being termed sandy loams, whilst those with a majority of clayey particles are described as clayey loams. Such soils usually contain little carbonate of lime (*i.e.* are non-calcareous), but there are clayey soils which are calcareous (*i.e.* with a considerable amount of chalk), the so-called *marls*, whilst a still larger amount of lime is present where the subsoil itself consists of chalk or limestone. A sandy soil differs from the sandy gravels mentioned above in the smaller average size of its particles, which generally compose the entire soil to the exclusion of clay; examples are furnished by the wind-blown sand of dunes and the soil of the Breckland district of Suffolk.

Most soils contain a certain amount of humus which imparts to them their dark colour, and it is this which more or less sharply distinguishes the true soil from the subsoil, *i.e.* the half-decomposed surface of the underlying rock which is in process of being converted into soil. On the exposed face of railway cuttings, etc., soil, subsoil and underlying rock are often readily recognised (see Fig. 34).

As a general rule no very great amount of organic material is present, although a thin layer of almost pure humus is often found at the surface, but in woodland-soils and garden-mould, for instance, a much larger quantity occurs. Such humus is almost completely disintegrated, largely owing to the action of Earthworms, whereas the *peat* which is found in moorland

districts consists of vegetable remains which have undergone little change and moreover often accumulate to a great depth (see p. 324).

From the point of view of the plant the important characteristics of a soil are its capability to furnish the necessary mineral salts, its air-content and its power of absorbing and giving up water. The last feature may be considered at once. We have seen that the water is held as a thin film round each

FIG. 34.—Photograph to show soil (*a*) and subsoil (*b*). The strip of white paper represents a length of 1 foot. No-man's-land, Hertfordshire. [Photo. E. J. S.]

particle and therefore a fine-grained soil, offering as it does a much larger total surface for the water-films than a coarse-grained one, will hold a greater quantity than the latter. This fact can be shown in the following way.

A number of small holes are drilled in the bottoms and lids of two equal-sized tins, after which one is filled with a clayey and the other with a sandy soil, neither being completely dry.[1] The two tins are then placed in a shallow bowl which is filled

[1] Since moisture passes only very slowly into completely dry soils.

with water to the depth of about half an inch, and left for an hour during which the water may have to be renewed. Thereupon they are removed, the excess of water is allowed to drip off and each tin with its soil is weighed. After that, both tins are heated in the way described on p. 63 until all the water has been driven off, and reweighed. The difference between the first and second weighings will show that the *water-capacity* of the clayey soil is considerably greater than that of the sandy one. It is instructive to compare other soils in the same way.

When water is absorbed by the root-hairs of a plant, the latter, as we shall see (p. 108), exert an attraction on the film around those soil-particles with which they come into close contact, and thus have to overcome the attractive force which holds the film to the surface of the particle. But as the water-film becomes thinner, this retentive power increases and consequently at a certain stage of dryness the moisture is held by the soil-particles so firmly that the roots cannot absorb it. In a fine-grained soil owing to the much larger film-surface this state will be reached when quite a considerable amount of water still remains, whereas in a coarse-grained soil with its smaller surface the amount of moisture left when the films have thinned out to this limit will be relatively small. We must therefore distinguish between the *available* and *non-available* water, the latter being that which is left in the soil and which can be driven off by heating after plants growing in it show signs of wilting. Whilst a fine-grained soil still containing 12 per cent. of water may already be dry from the point of view of the plant, a coarse-grained one with 5 per cent. of water would still probably provide sufficient moisture.

There are two principal sources of the water in the soil: the greater part comes directly from the atmosphere above and is absorbed as it slowly trickles through the earth, but in many cases part of the moisture is drawn up by attraction (capillarity) from the underground water-table. Considering the former point first, we may notice that different soils vary greatly in the facility with which they permit the water that falls on their surface to pass through them—in other words, their *permeability* differs. Thus, a coarse-grained sandy soil allows water to drain very rapidly through the large spaces between

the particles, so that but little is retained; in such a soil, however, the interspaces are always occupied by air and there is no risk of water-logging (unless the soil be shallow and situated upon some impermeable layer). The greater the percentage of fine-grained particles the less permeable does the soil become; the water passes through very slowly, tends to accumulate in the interspaces, and consequently in such a case there is always a danger of inadequate aeration. A clayey soil, for instance, when once thoroughly wet, comes to be almost impermeable, a property made use of in the puddling of ponds. This is readily shown by the following experiment (Fig. 35).

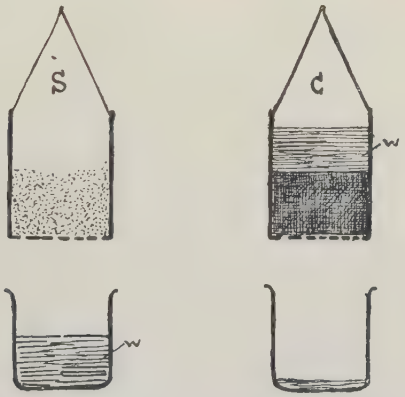


FIG. 35.—Experiment to show relative permeability of sand (*S*) and clay (*C*) to water (*W*). The water in the two beakers is shown as it would appear at the end of the experiment.

Two small tins have their bases perforated by a number of fine holes and are then half filled with closely packed sandy and clayey soils respectively. Both are then suspended over tumblers, and an equal volume of water is added to each. It will be observed that in a given space of time far more water runs through the sandy than through the clayey soil (Fig. 35), and indeed the latter may be found to be quite impermeable. It will be realised, therefore, that coarse-grained soils contain little water but are well aerated, while fine-grained soils have plenty of water but tend to be badly aerated, so that a soil with a duly balanced amount of coarse and fine particles

(*e.g.* a loam) will give the most satisfactory combination as regards water- and air-content.

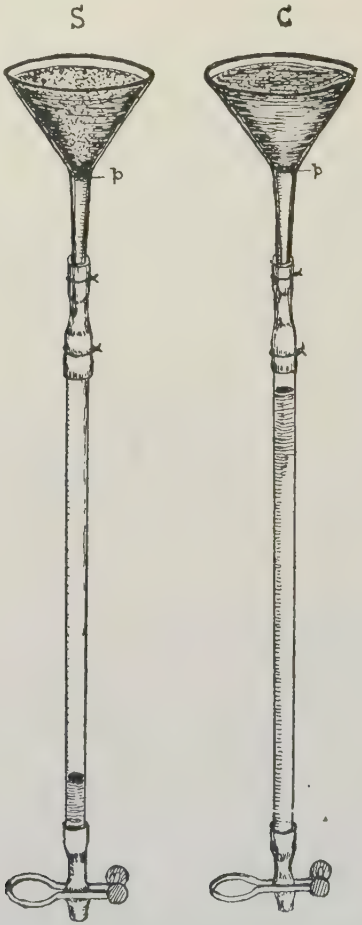


FIG. 36.—Experiment to show relative permeability of sand (*S*) and clay (*C*) to air. *p*, plug of cotton-wool. The level of the water in the two tubes is shown as it would appear at the end of the experiment.

The permeability of different soils to air can be compared in the following way (Fig. 36): An ordinary glass-funnel is filled with closely packed wet clayey soil which is prevented

from extending into the stem of the funnel by a small pad of cotton-wool (*p* in the figure). A piece of glass tubing, slightly wider than the stem of the funnel, is fitted at each end with a short length of rubber tubing, one of these being closed with a clip. The glass tube is now filled with water and attached by the second piece of rubber tubing to the stem of the funnel, so as to make an air-tight connection (Appendix VII.) A second perfectly similar apparatus is fitted up, in this case, however, employing a wet sandy soil. The clip closing the base of each tube now being opened, the water rapidly runs out of the apparatus containing the sandy soil, through which air has passed to take its place, whilst little or none escapes from that containing the clay.

As regards absorption of moisture by *capillarity* from the underground water-table, this is of course only possible where the level of the latter is not too deeply situated. Such raising of the water is mainly of importance in times of prolonged drought, when abundant evaporation from the surface-layers of the soil brings about a kind of suction from below. Inasmuch as the air-spaces form one continuous system, they constitute a series of capillary channels through which the water rises. The height to which the water can be drawn, however, depends on the small size of these spaces, and therefore such capillary suction comes into play much more effectively in a fine-grained clayey soil than in a coarse-grained sandy one.

That this is the case can be demonstrated by selecting two glass tubes, open at both ends (about 2 feet long and half an inch in diameter), and closing one end of each with a piece of muslin (Fig. 37); one tube is then filled with dry sand and the other with dry, finely divided, clay, the lower (closed) end of each tube being immersed in water. By slow degrees the moisture travels upwards, but it moves more rapidly and reaches a greater height in the clay than in the sand.

We have just referred to the fact that evaporation of water goes on from the surface of the soil, but its amount depends on a great many features. In the first place, what has been said above about the strength of attraction between the particles and the water-films has an important bearing on this matter, since in evaporating the water has to overcome this attractive force which, as already explained, increases as the soil becomes

drier. The nature of the surface also plays a great part in determining the amount of evaporation. If the surface is kept finely divided (*e.g.* by ploughing, raking, etc.),—in other words, is kept in good tilth,—the uppermost layer of the soil will be dry, but will consist of numerous loose particles with large air-spaces between them. This surface-layer or *mulch* of dry well-aerated earth prevents evaporation, inasmuch as the number of

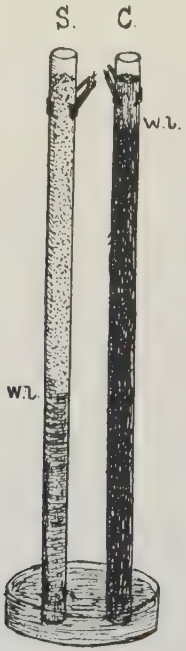


FIG. 37.—Experiment (after Russell) to demonstrate that clay is more effective in raising water by capillarity than sand. *C*, clay ; *S*, sand ; *W.l.*, water-level.

fine capillary tubes has been greatly diminished; so that, whilst absorption of water by capillary suction goes on as readily as before up to the level of the mulch, the loss from the latter is much less ; furthermore, the interchange of gases between soil and atmosphere is facilitated.

A surface-crust provides numerous capillary channels for the upward passage of the evaporating water, besides impeding

the ready gaseous exchange between soil and air. An instructive experiment can be performed to illustrate this fact. Two pots are filled with some moist clayey soil and weighed, the surface-layer in the one being kept finely divided, whilst that in the other is pressed down to form a crust. The latter will be found to lose weight much more rapidly than the former. It may be added that in gardens, besides the broken surface of the soil itself, mulches of straw and dung are often employed.

There is one other feature that must still be noticed in order to complete our knowledge of the physical characteristics of the soil. Clay swells up when wetted and becomes highly sticky, and it is this property of swelling which is largely responsible for its impermeability to water and air in this condition. As a result, every soil that contains any considerable proportion of clayey particles is very hard to dig and is spoken of as a *heavy* soil, in contrast to coarse-grained soils, with little cohesion between the particles, which are easy to dig and are termed *light* soils.

It is, however, possible to modify the characteristics of clayey soils—in other words, to make the heavy soil lighter—in one of several ways. The simplest (which is, however, difficult to apply on a large scale) is to add a certain amount of sand and to mix this thoroughly with the clay. A method extensively employed in this country is to add a top-dressing of lime, for which chalk is often substituted. This has the effect of diminishing the cohesion of the clayey particles and thus of increasing the permeability. Whereas clay will remain in suspension in a vessel of water for days, the water soon clears if 10 per cent. lime-water (or a little acid) be added. Humus also helps to lighten a heavy soil and is occasionally employed in gardens in this way, although it is hopeless attempting to effect much with humus alone, if the soil be very clayey.

Just as the addition of sand to a heavy soil tends to increase its air-content and to diminish its water-retaining power, so can a sandy soil be improved in the latter respect by adding clay. The mixing of humus with a sandy soil also considerably increases the water-capacity, which at first appears to be anomalous, since humus is used also to lighten soils. The latter application depends on the relatively large size of the humus-particles, whilst their spongy character is

responsible for the marked retention of water, a fact which is especially obvious in the case of peat.

The addition of humus to a soil is also of importance to the plant owing to the valuable food-substances which it contains. In fact, a sandy soil without humus furnishes practically no food at all. In clayey soils a good deal more of the nourishment that plants require is present, though not always readily available.

Under natural conditions plants (and animals) die and rot on the soil on which they have lived, and much of the substance which they have taken from the ground returns to it again in the form of humus and other products of decay. In the case of cultivated land, however, this does not apply; a greater or smaller portion of the body of the plant is removed and so year by year the soil gets more and more impoverished. Hence the necessity, under cultivation, for the frequent application of manures which serve to replenish the stock of mineral food-substances required by the plant for building up its body.

It may finally be noticed that there is a certain relation between the character of the soil and the root-system of the plants inhabiting it, since in a light soil (*e.g.* that of a sand-dune) the roots tend to be much more extensive than in a heavy one. This may be demonstrated by filling half the glass-fronted box described on p. 54 with a light soil and the other half with a heavy one and planting seeds against the glass, when the stronger development of the root-systems of the seedlings growing in the light soil will soon be apparent.

CHAPTER VII

The Architecture of the Shoot

The shoot, as we have already learnt, in the majority of cases grows erect in obedience to the directive influences of light and gravity (p. 17), though occasionally it may exhibit a prostrate or climbing habit (see Chapter II.). Quite apart, however, from these broad distinctions the shoot differs greatly in appearance from plant to plant, so that we are generally not at a loss to know one kind from another. This variety of form is determined by the way in which the stem branches, by the mode of arrangement of the leaves and by their shape, and we shall therefore not be in a proper position to understand the architecture of the shoot until we have considered all these points separately.

It is easiest to study the mode of branching in the first place on woody plants, because the succession of events is more clearly seen in them than in herbs which frequently do not branch much until the time of flowering. If we examine a woody shoot, as for instance one of the larger branches of the Beech, in winter-time (Fig. 38 A), we find that it is terminated by a long, slender and pointed structure of a brown colour, the *terminal bud* (*t.b.*); this contains in miniature and telescoped together next year's continuation of the branch. Along the sides of the latter are a number of perfectly similar buds (the *lateral buds*, *l.b.*), each capable in the next season of growing out into a side-branch. Beneath each lateral bud the bark shows a somewhat kidney-shaped smooth scar (*l.s.*), generally well defined and bearing a curved band of dots. Each scar marks the former point of attachment of a leaf (*i.e.* it is a *leaf-scar*, see also Fig. 40), and the dots on its surface are the broken ends of the strands joining stem and leaf (p. 8). It will be seen, therefore, that the

lateral buds are all axillary (p. 2) to leaves of past seasons, the terminal buds alone having no subtending leaf-scars.

The colour and shape of buds and leaf-scars and the mode of arrangement of the strands on the latter varies so much in

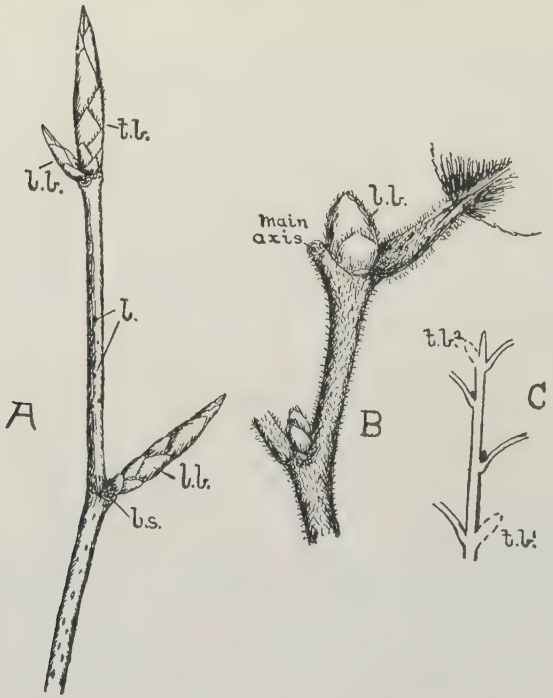


FIG. 38.—A, Portion of a twig of Beech in winter-time (about natural size). B, Ditto of Elm (somewhat enlarged). C, Diagram to explain behaviour of terminal bud in the Elm or Lime. *l*, lenticels; *l.b.*, lateral buds; *l.s.*, leaf-scar; *t.b.*, terminal bud; *t.b.*¹ and *t.b.*² in Fig. C, terminal buds of successive seasons which die away.

different trees and shrubs that it is not difficult to recognise them in winter by such characters. Other external features are provided by the *lenticels* (Fig. 38 A, *l*; Fig. 40), small generally lighter-coloured projections of varying shape, which are irregularly distributed on the bark of woody plants and serve the purpose of gaseous interchange between the interior of the

branch and the atmosphere, prevented except at these points by the impermeable bark.

The most fundamental point of distinction in the mode of branching lies in the behaviour of the terminal bud. In a considerable number of trees, of which the Conifers (*e.g.* Spruce Fir, Larch, Cypress, etc.) furnish excellent examples, the original plumule of the seedling steadily continues its growth year by year, lengthening out in the spring and producing a new ter-

Fig. 39.—Photograph showing monopodial growth of two typical Conifers. The one in the centre is the Monkey Puzzle (*Araucaria imbricata*); the right-hand one is Arbor Vitæ (*Thuja*). [Photo. E. J. S.]

minal bud in the autumn, so that a tall, straight, main axis (or monopodium) is produced. A certain number of lateral buds develop into side-branches of the first order, but these are all subsidiary to the central shaft and again branch in the same manner. Moreover, in this method of *monopodial* branching the oldest and largest laterals are farthest away from the growing tip, whilst the youngest and smallest are close to it. As a result of this very regular branching, such plants often exhibit

a very symmetrical conical shape (Fig. 39), well seen in a good specimen of a Christmas tree.

The most essential characteristic of the type just considered is the persistence of the growing point of the main axis from year to year, and herein lies the distinction from so-called *sympodial* branching. This latter is seen in its simplest form in the Elm (Fig. 38 B and C) or Lime. If a branch of one of these trees be examined in the course of the summer, it will be found

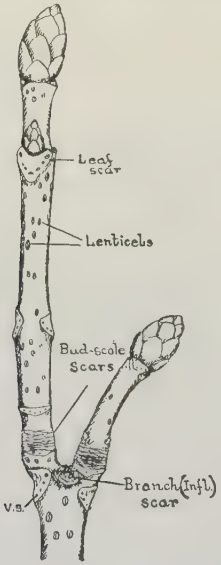


FIG. 40.—Portion of twig of Horse Chestnut showing buds, leaf-scars and lenticels (about two-thirds natural size). *v.s.*, vascular strands.

to possess a well-marked terminal bud, but as the season advances this bud begins to show signs of withering, while the axillary bud situated just beneath it increases in vigour. Ultimately, when the winter arrives, this latter will be found to occupy a position at the extreme end (Fig. 38 B, *l.b.*), the true terminal bud being represented by a small shrivelled remnant or scar (main axis in Fig. 38 B) at one side. Careful examination even at this time, however, shows that the bud at the end of the branch is not a true terminal one, since beneath it is found a leaf-scar (cf. p. 74).

The lateral buds which thus always come to occupy the ends of the branches in the Elm or Lime continue the growth of the latter in the following season, so that as the years go on there is built up a false axis or sympodium, consisting of a succession of lateral branches, so adjusted as to form an apparently continuous whole (cf. Fig. 38 C). In other cases, however, sympodial branching does not take place with such regularity.

In the Horse Chestnut (Fig. 40), for example, a good deal of monopodial branching takes place, and sympodial branching

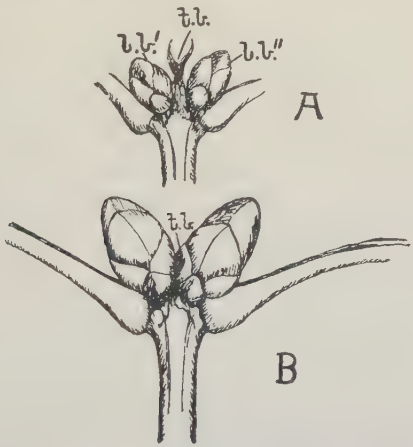


FIG. 41.—Twigs of Lilac illustrating dichasial branching and dying away of terminal bud. A, Young stage, about natural size. B, Older stage, slightly enlarged. *l.b.'*, *l.b."*, lateral buds; *t.b.*, terminal bud.

occurs only in connection with flowering. The inflorescence (p. 6) of this tree forms the termination of the branch upon which it is borne; when flowering and fruiting are over, the stalk of the inflorescence dies away and leaves a large round somewhat sunken scar (Fig. 40, infl. scar), whilst the nearest lateral bud shifts into the line of continuity and in the next season replaces the branch whose further growth terminated with the production of flowers. Scars marking the former points of attachment of inflorescences are always to be found on branches of the Horse Chestnut and must be distinguished from the horseshoe-shaped leaf-scars (Fig. 40).

The Lilac (Fig. 41) shows a slightly different type of sympodial branching. Here the terminal bud usually, though not invariably, dies away, or its existence is terminated by the formation of an inflorescence, as in the Horse Chestnut. The difference, as compared with the cases previously considered, lies in the fact that two lateral buds, instead of one, grow out to replace the main axis, so that it looks as if the latter had forked. This so-called *dichasial* branching is also well seen in the Mistletoe.

The extent to which branching is carried on varies greatly; on the one hand we have plants, like most Monocotyledons, in which it is practically restricted to the region of the inflorescence, whilst on the other we have richly branching trees, such as the Beech or Elm. In all woody plants, however, the materials available for growth suffice for the development of only a small number of the buds, a very considerable percentage being doomed to inactivity, either permanent or temporary. These inactive or *dormant buds* retain their vitality often throughout the life of the tree or shrub and are ready to grow out into branches, should occasion demand. That it is lack of nourishment which in many cases prevents them from developing further is easily seen if we remove the terminal portion of any given branch; thereby lateral buds borne lower down upon it which would otherwise remain dormant are caused to sprout. Upon this depends the principle of hedge-making, in which by cutting off the tops of the upper branches numerous laterals are caused to develop, so that a dense growth results.

In a few plants (*e.g.* Scotch Fir, Field Spurrey, Fig. 42) most of the lateral branches do not elongate in the normal way, but remain quite short owing to the non-development of the internodes; such branches are termed *dwarf-shoots* (Fig. 42, *d.s.*). Most of our fruit-trees exhibit a similar phenomenon, but here a few of the lower internodes are developed, so that these *spur-shoots* do not remain quite as short as typical dwarf-shoots. In woody plants showing these features most or all of the axillary buds sooner or later develop into branches, *i.e.* there are few or no dormant buds on the older parts of the plant; the majority of the branches remain arrested in the manner already described, although a certain number (in the case of the Scotch Fir, confined to the tip of each year's growth)

give rise to long shoots. Here again it appears to be lack of nourishment that leads to the limited development of the dwarf- or spur-shoots, since removal of the tip of the main branch leads to an elongation of one or more of the latter.

In the case of the root we found that the laterals arose

FIG. 42.—Branch of the Field Spurrey, showing dwarf-shoots (*d.s.*) (about two-thirds natural size).

endogenously (p. 53, Fig. 28 A and B), but the branches of the stem, as also the leaves, are readily seen to originate from the surface-tissues only (cf. Fig. 28 C and D, Fig. 49), *i.e.* they are *exogenous*. The protection afforded to the young lateral root as a result of its internal origin is unnecessary in the case of the branches of the stem, where no such resistance, as the soil offers to the growth of the root, has to be encountered. This also

accounts for the region of elongation of the shoot being much longer than in a root (cf. p. 50).

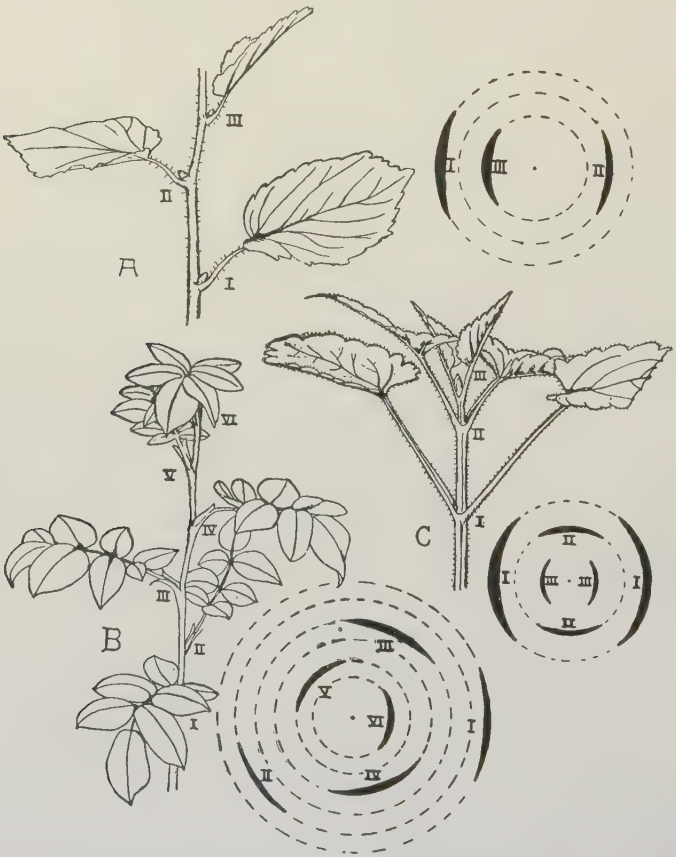


Fig. 43.—Shoots and diagrams to show leaf-arrangement. A, Hazel (leaf-arrangement $\frac{1}{2}$). B, Dog-rose (leaf-arrangement $\frac{2}{5}$). C, Hedge Woundwort (leaf-arrangement decussate). In the diagram the dotted circles represent successive nodes, the leaves being indicated in black and numbered in correspondence with the leaves of the shoots.

In all the above examples we have spoken of shoots as arising from normal buds developed in the axils of leaves. Exceptionally, however, shoots may originate in another way, as, for

example, from the cut stumps of trees, from roots (*e.g.* in the Bindweed and Poplar) or from foliage-leaves (*e.g.* the Milkmaid and some cultivated Ferns). The term *adventitious*, which we have already applied to roots (p. 57), is used also for such shoots, developing in an abnormal position.

The majority of plants exhibit but a single leaf at each node, an arrangement which is described as *alternate*, but there are quite a large number of plants (*e.g.* Horse Chestnut, Fig. 40; Lilac, Fig. 41; Hop, Fig. 11; Hedge Woundwort, Fig. 43 C; Chickweed) in which a pair of leaves arise together, when the leaf-arrangement is said to be *opposite*. Such pairs of leaves almost invariably occur at right angles to one another at successive nodes (Fig. 43 C), *i.e.* they are *decussate*. Occasionally, as in the Teasel and Yellow Centaury, the bases of the two opposite leaves (which are here sessile, p. 5) are joined together so as to surround the stem, a condition described as *connate*. If more than two leaves occur at a node the group is spoken of as a *whorl*, examples being seen in the Oleander and the Water Milfoil; here again the leaves of one whorl usually alternate with those above and below. The object of such alternation between the leaves of successive nodes is to prevent undue overshadowing, and the same end is attained in the case of alternate leaves by their spiral arrangement (cf. below).

In many herbaceous plants (*e.g.* Dandelion, Shepherd's-purse, Fig. 1) a large number of leaves arise close together from the base of the stem just above the surface of the soil; such leaves are usually collected in the form of a rosette and are described as *radical* leaves (Fig. 1, *r.l.*), in contrast to those borne on the upper part of the stem, the *cauline* leaves (Fig. 1, *c.l.*).

The simplest possible type of alternate arrangement is for one leaf to be separated by half the circumference of the stem from that at the next node, so that the leaves form two vertical rows. This *distichous* arrangement is well seen in the Hazel (Fig. 43 A), in Grasses and in the Ivy (Fig. 31) and is often expressed simply by the fraction $\frac{1}{2}$. In the Beech and in Sedges, for instance, the leaves are closer together, forming three vertical rows on the stem and being separated from one another by only one-third of the circumference; the arrangement is therefore *tristichous* and can be briefly represented by the

fraction $\frac{1}{3}$. One of the commonest types is for successive leaves to follow at intervals equal to two-fifths of the stem's circumference (Fig. 43 B). These more complicated leaf-arrangements are best studied in the following way.

Starting with a leaf near the base of the branch we begin by tying one end of a piece of white cotton to its petiole; we then carry on the cotton to the next leaf above, which we approach by the shortest path, and after twining the cotton once round the leaf-stalk, pass on to the next, and thus proceed until we reach a leaf situated vertically above the one with which we started. If this is carried out on the branch of a Rose (Fig. 43 B) or a Poplar, we shall find that our cotton traces out a spiral line which passes twice round the stem, and that, from one leaf to the next one vertically above it, the thread traverses five internodes. A little consideration will show that in these plants therefore each leaf must be separated from the neighbouring one by an interval equal to two-fifths of the circumference of the stem (see also the ground-plan in Fig. 43 B). In other cases the leaf-arrangement is $\frac{3}{8}$, that is, our cotton-spiral would encircle the stem three times and traverse eight internodes; radical leaf-rosettes (*e.g.* of the Plantain) often display this very clearly.

It should be added that in plants having a spiral leaf-arrangement the interval between successive nodes is often not a constant one throughout the plant, so that, for instance, a $\frac{2}{5}$ arrangement below may give place to a $\frac{1}{3}$ above (*e.g.* in the Poplar). It is, however, important to realise that alternate leaves are not scattered irregularly on the shoot, but are disposed according to some definite, even though slightly variable, plan.

The external form of the stem often varies with the arrangement of the leaves upon it; thus, although in most plants having alternate leaves the stem is cylindrical, the $\frac{1}{3}$ arrangement in Sedges is associated with a triangular stem, whilst in plants with decussate leaves the stem is often square (*e.g.* Dead-nettle, Hedge Woundwort, Fig. 43 C; Scarlet Pimpernel).

In the case of erect shoots or of rosettes the leaves retain throughout life the position which they occupied at their first development and which is generally well suited to prevent overshadowing. But in the case of the horizontal branches of trees and shrubs the matter is different; the leaves show the

same original arrangement as on the upright branches, but during development this becomes more and more obscured and replaced by an arrangement more suited to the direction of illumination. This is very clearly seen, if one compares an upright and horizontal branch of a Privet or other plant with opposite leaves. On the erect branch the decussate character is quite distinct, but on the horizontal one the leaf-stalks have

FIG. 44.—Photographs of two branches of the Hornbeam; on the left a horizontal branch showing leaf-mosaic, on the right an upright shoot showing radial arrangement of the leaves. [Photo. E. J. S.]

twisted, so that the blades are placed more or less horizontally at right angles to the light, the original position of the leaves being only made out by a careful scrutiny of their mode of attachment.

The same feature can be observed in the Beech, where on the side-branches the leaves all appear in one plane instead of three; another good example is furnished by the Hornbeam (Fig. 44). Whilst leaves are able to adjust their position in

this way before they attain to maturity, this is not usually possible after the leaf is fully grown (see, however, p. 91); a position is therefore taken up during development, such as is best suited to light-reception.

The preceding considerations indicate that we must distinguish between shoots in which the leaves and branches spread out in all directions from the central axis (*radial* shoots, *e.g.* in most erect plants), and those in which the leaves and

FIG. 45.—Photograph of seedling Sycamore taken from above to show leaf-mosaic. [Photo. E. J. S.]

branches lie in one plane (*dorsiventral* shoots, *e.g.* horizontal and creeping stems). For, in the latter case, the axillary buds tend to grow out in the plane of the leaves, as is well seen in the horizontal branch-systems of Hornbeam (Fig. 44), Elm or Beech. In fact, there is here one almost continuous expanse of leaf-surface, smaller leaves being situated between the larger ones and those of neighbouring branches overlapping only to a very slight extent, so that we can speak of a *leaf-mosaic*, a feature which is always pronounced in trees with a dense canopy and

in smaller plants growing in the shade of larger ones. Such leaf-mosaics are also exhibited by radial shoots (*e.g.* in seedlings of the Sycamore, Fig. 45).

The foliage-leaf [1] as a general rule consists of three parts: the base or slightly enlarged attachment to the stem, the stalk or petiole whose upper surface is generally grooved or flat (Fig. 54), and the blade or lamina. Occasionally the petiole is absent, as, for example, in the upper *sessile* leaves of the Shepherd's-purse (p. 5, Fig. 1), but the majority of leaves are *petiolate*. The petiole plays an important part, not only as an organ for spreading out the blade to the light and air, but also as we have just seen by placing the latter in the most suitable light-position; it also serves as a means of communication between stem and leaf-blade, and through the hard vascular strands which traverse its length and join up on the one hand with the veins and on the other with similar strands in the stem (p. 8), food-substances travel to and from the leaf.

The leaf-blade may consist of one continuous undivided surface, in which case it is described as *simple* (Fig. 46 A, B, E); or it may be cut up into a number of lobes connected with one another by an undivided portion, when the leaf is said to be *lobed* (Fig. 45; Fig. 46 D); or again it may be completely segmented into a number of separate leaflets, when it is known as compound (Fig. 43 B; Fig. 46 C and H).

Diverse terms are used to describe the various shapes of leaves and leaflets. A prolonged description is, however, unnecessary, since Fig. 46 shows clearly what is meant by *linear* (*e.g.* Grass-leaves, Fig. 46 G), *lanceolate* (*e.g.* Privet, Fig. 46 I), *ovate* (*e.g.* Chickweed, Fig. 46 B), *obovate* (*e.g.* Garden Spurge, Fig. 46 F), *cordate* (*e.g.* Hedge Woundwort, Fig. 46 A), *reniform* (*e.g.* Ground Ivy, Fig. 46 E) and *hastate* (*e.g.* Convolvulus, Fig. 46 J). It will be noticed that the obovate shape of leaf is merely the ovate inverted, and similarly there are certain plants in which the blades take the form of an inverted heart and are described as *obcordate* (*e.g.* the leaflets of the Wood-sorrel, Fig. 126, p. 222). A peculiar type of leaf, termed *peltate*, is seen in the Pennyworts and the Garden Nasturtium (Fig. 66 B), the

[1] The internal structure of a typical foliage-leaf is described and figured on p. 129.

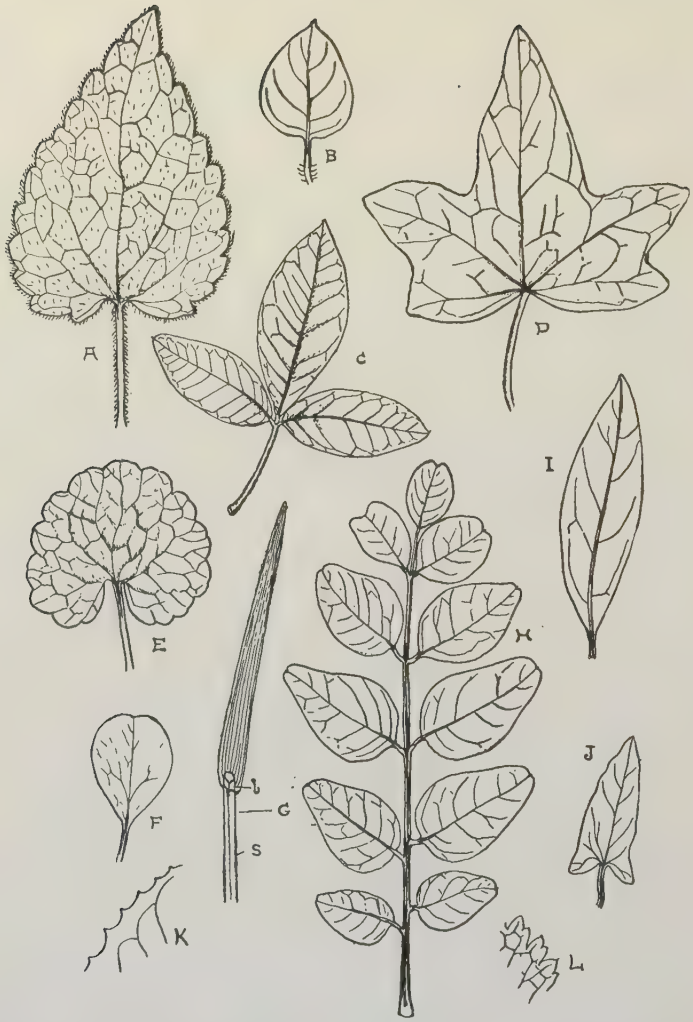


FIG. 46.—Different types of foliage-leaves (all about one-half natural size). A, Hedge Woundwort (cordate, acute). B, Chickweed (ovate, acuminate). C, Laburnum (trifoliate). D, Ivy (palmately lobed). E, Ground Ivy (reniform, crenate). F, Garden Spurge (obovate, obtuse). G, Grass (linear). *l*, ligule; *s*, leaf-sheath. H, False Acacia (*Robinia*) (pinnate with mucronate leaflets). I, Privet (lanceolate, entire). J, Field Convolvulus (hastate). K, Enchanter's Nightshade (showing dentate margin only). L, White Dead-nettle (showing biserrate margin only).

petiole being here attached to the centre of the round blade. A somewhat similar form occurs in the Garden Geranium in which the base of the lamina is drawn out into two lobes which almost meet in the middle line (*orbicular*). As a general rule the two halves of the blade are identical in size, but when one is larger than the other (*e.g.* Lime or Elm) the leaf is said to be *asymmetrical.*

Terms are similarly employed to describe the margin of the leaf ; this may be either *entire* (Fig. 46 B, F, I), *i.e.* with a smooth uncut outline, or *serrate* (Fig. 46 A) with forwardly directed or *dentate* (*e.g.* Enchanter's Nightshade, Fig. 46 K) with outstanding teeth, or *crenate* (Fig. 46 E) with rounded projections. When the margin is provided with fine hairs, as in the Beech and Woundwort (Fig. 46 A) it is said to be *ciliate,* whilst when there are teeth of two sizes it is described as *biserrate* (*e.g.* the White Dead-nettle, Fig. 46 L) or *bidentate.*

The nature of the leaf-tip also varies, but here again the figures will make quite clear as to what is meant by *acute* (Fig. 46 A and I), *obtuse* (Fig. 46 F), *acuminate* (*i.e.* tapering to a point, Fig. 46 B) and *mucronate* (*i.e.* with a small point arising from an almost straight edge, as in the leaflets of the False Acacia, Fig. 46 H). The surface of the leaf is either *leathery* (as in the Laurel), without hairs (i.e. *glabrous,* as in the Privet), *hairy* (as in the Woundwort), or *glaucous* (*i.e.* with a bloom, as in the Sea Holly).

We have noticed in the Shepherd's-purse (p. 5, Fig. 3) that the extent of lobing of the leaf-blade varies greatly, and this shows us that there is no essential difference between a serrate or crenate margin on the one hand and a deeply lobed margin on the other. In many plants, however, the character of the margin is quite constant, and therefore it is often convenient to employ special terms for deeply cut leaf-blades, *e.g.* the *sinuate* margin of the Oak or the *palmately lobed* leaves of the Ivy (Fig. 46 D) and Hop (Fig. 11), in which the lobes are arranged like the fingers of a hand. If we imagine such lobing to extend inwards to the midrib, a compound leaf would result.

Two principal types of the latter can be distinguished : that in which the leaflets or *pinnae* are arranged in two rows, one on either side of the leaf-stalk (*pinnate,* Fig. 46 H ;

Fig. 43 B), and that in which all the leaflets come off from the same point (*palmate*, as in the Horse Chestnut). In the former type the petiole either terminates in a leaflet (*e.g.* Sainfoin, Ash, Rose, Fig. 43 B), or such a terminal pinna is wanting (*e.g.* Bitter Vetch). A common form of leaf is that shown by the Strawberry (Fig. 85), Clover, Laburnum (Fig. 46 C), etc., in which only three leaflets occur, when the blade is said to be *trifoliate*. Occasionally the leaflets of compound leaves themselves exhibit subdivision, so that we have blades which are *bipinnate* (*e.g.* Beaked Parsley, Acacia, Fig. 126 A) or even *tripinnate* (*e.g.* many Ferns). Compound leaves are readily distinguished from branches bearing small leaves by the presence of a bud in the axil of the main stalk,[1] by the absence of axillary buds to the individual leaflets, and by the absence of a terminal bud.

The transition of foliage already noticed in the Mallow (p. 46) indicates that the leaves of an individual are not necessarily all alike in form, and some plants indeed, as for instance the Ivy and the Goldielocks, regularly produce foliage of two types. In the former the lower leaves are palmately lobed, whilst those upon the flowering branches are more or less oval in outline; in the second example the radical leaves are approximately orbicular, but those upon the stem are deeply cut into a number of narrow segments.

We may conclude our discussion of the leaf-blade by a brief consideration of the manner in which the veins are arranged (*i.e.* the *venation*). In the Shepherd's-purse we noticed that each leaf showed a prominent main vein or midrib, giving off a number of lateral veins which by continued branching formed a network throughout the lamina (Fig. 3). Such *reticulate* venation is characteristic of the leaves of most Dicotyledons, but differences are found as regards the way in which the prominent veins are distributed. Most commonly a single midrib is predominant and from it laterals of smaller size arise on each side (*pinnate* venation, Fig. 110 and Fig. 46 B and I), but occasionally there are several veins of equal prominence branching out from the base of the blade like the fingers of a hand (*palmate* venation, Fig. 46 D and E).

[1] In most Ferns buds are not formed in the axils, but on the backs of the bases of the leaves.

In most Monocotyledonous leaves a totally different type of venation is found; the blade is traversed by several equal veins running side by side and connected with one another by numerous cross-branches, the venation being described as *parallel* (Fig. 46 G).

CHAPTER VIII

Buds. The Mechanical Structure of the Shoot

We have still to consider the *leaf-base* which exhibits great variety of form and fulfils quite a number of different functions.

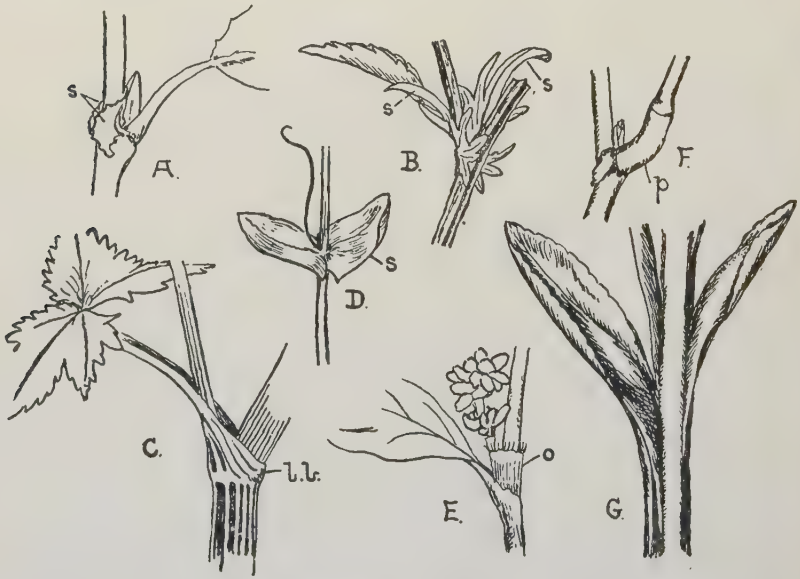


Fig. 47.—Leaf-bases and stipules of various plants (all about natural size). A, Willow, summer-shoot. B, Pansy. C, Burnet Saxifrage (*Pimpinella magna*). D, Meadow Vetchling (*Lathyrus Aphaca*). E, Persicaria. F, Runner Bean. G, Mullein (decurrent leaves). *l.b.*, leaf-base; *o*, ochrea; *p*, pulvinus; *s*, stipule.

In a large number of plants it appears merely as a more or less marked enlargement at the base of the leaf serving for

its attachment to the stem (*e.g.* Lime and Castor Oil). In some cases this enlargement is more extensive, forming a prominent cushion or *pulvinus*, and in such leaves the base often retains the power of bending throughout life, so that they are able to adjust their position repeatedly with reference to the light; examples are furnished by the pulvinus at the base of the petiole in the Runner Bean (Fig. 47 F, *p*) and at the base of the leaflets in the Wood-sorrel (Fig. 126) and False Acacia. In the last two plants especially the leaflets droop down at night, recovering their normal position on exposure to light; such sleep-movements will be considered more fully in a later chapter (p. 221).

Plants possessing large blades often exhibit special modifications of the leaf-base to enable them to withstand the great strain entailed by the resistance offered to wind and rain by the extensive leaf-surface. A simple example is afforded by the Sycamore, in which this is met by a mere swelling of the leaf-base, but in a large number of cases (*e.g.* Hogweed, Burnet Saxifrage, Fig. 47 C, and other plants of the same family, Grasses) the base is expanded to such a degree that it extends round the stem on either side as a more or less close-fitting *leaf-sheath* (Fig. 47 C, *l.b.*), the margins of which in Grasses [1] (Fig. 46 G, *s*) actually overlap. It will be plain that, since the lower edge of such a sheath is attached to the node along its whole circumference, a much firmer connection between leaf and stem is obtained without loss of elasticity. An extreme type is seen in the Sedges where the leaf-sheath forms a closed tube enveloping part of the internode above, the blade, as in Grasses, actually diverging from the stem only at some distance above the node. In the Buttercup-family, on the other hand, the sheath is not so well developed, extending only about half-way round the stem. A further method of increasing the connection with the stem is found in the Mullein (Fig. 47 G) and Cotton-thistle, where the lower part of the sessile blade is joined up with the axis, such a leaf being described as *decurrent*.

[1] A peculiar structure, of varying size and shape and generally of a membranous texture, is present at the junction of blade and sheath in Grasses (Fig. 46 G, *l*). The purpose of this *ligule* is not properly understood, but it is supposed to be in some way or other protective in function.

In all those cases in which the leaf-base is enlarged it affords a certain amount of protection to the axillary bud, and this is very pronounced in the swollen sheath of the Hogweed, etc. (Fig. 47 C). A very efficient protection of axillary buds is shown by the Ivy (Fig. 31), the Plane-tree and the Syringa (Fig. 48 B), in all of which the hollow leaf-base more or less surrounds the bud, so that the latter is not visible until the leaf has been removed (see right-hand diagram in Fig. 48 B). The

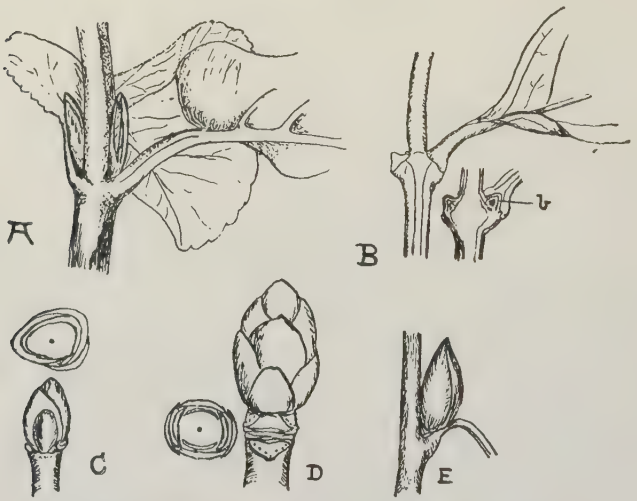


FIG. 48.—Bud-protection (all figures about natural size). A, Wayfaring Tree (naked buds). B, Syringa (*Philadelphus*) (bud in hollowed petiole). C, Lime-bud, with plan of bud-scale arrangement above. D, Horse Chestnut-bud, with plan of bud-scale arrangement at side. E, Goat-willow. *b*, bud.

value of the leaf-base as a protective structure depends in part on the fact that this portion of the leaf reaches maturity very early, and this consideration is specially important in those cases in which it bears leafy outgrowths or *stipules* (Fig. 47 A and B) which help to shield the axillary bud. Leaves possessing such structures are described as *stipulate* in contrast to leaves in which they are absent, which are said to be *exstipulate.*

Simple forms of such stipules are found, for instance, on

the summer-shoots of Willows (Fig. 47 A, *s*), in the Cherry and in the Garden Geranium, whilst larger ones, which in this case are deeply lobed, are seen in the Pansy (Fig. 47 B, *s*); the Rose-leaf (Fig. 9 B, *s*; Fig. 43 B) has its stipules joined up with the petiole, so that the base of the latter appears winged. In many plants the stipules are green and thus assist in the assimilatory function (p. 11) of the blade; such stipules generally remain attached throughout the life of the leaf (*i.e.* they are *persistent*), whilst when merely protective they are often leathery or membranous and usually fall off at an early stage (*i.e.* they are *caducous*). Plants in which the blade is modified for other purposes (*e.g.* to form tendrils for climbing, as in the Meadow Vetchling, Fig. 47 D), often exhibit a great development of the stipules which then constitute the only assimilatory portion of the leaf.

As a general rule the stipules can be easily recognised as arising directly from the leaf-base, but occasionally they appear rather as outgrowths from the stem on either side of the node; in all such cases, however, they can be distinguished from leaves by the fact that there is no bud in their axil. A very peculiar instance of this kind is furnished by the Goose-grass (Fig. 9 A) and the Bedstraws in which each node appears to bear a whorl of leaves; but careful examination shows that only two of these leaves situated opposite to one another ever possess axillary buds, and we can consequently infer that the other members of the whorl are stipules. The Knotgrass, the Persicaria (Fig. 47 E) and the Docks furnish other instances in which the stipules are not at once obvious, since here they are joined together so as to form a short membranous tube (*ochrea*) surrounding the axillary bud and the base of the internode above.

From a consideration of the mature shoot we can now pass to a study of its early development, material for which is furnished by every bud. The essential structure is always the same and may for the sake of convenience be examined in a Brussels Sprout,[1] a bud in which, owing to its large size, all the parts are easily recognised. Outwardly we see merely a series of overlapping leaves, but a more complicated structure is presented when the bud is halved lengthwise (Fig. 49). The central

[1] The Cabbage is likewise a huge bud, each Brussels Sprout being a Cabbage on a small scale.

portion is occupied by the stem which tapers to the growing point (*g.pt.*) above. On either side of the latter is seen a series of developing leaves (*p'*, *p''*, *p'''*, etc.), the youngest and

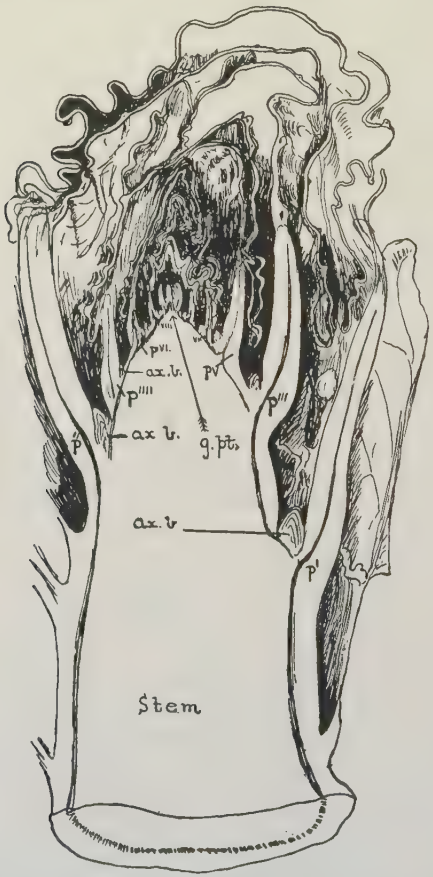


FIG. 49.—Section of Brussels Sprout (considerably enlarged). *ax.b.*, axillary buds; *g.pt.*, growing point of main axis; *p'*, *p''*, *p'''*, etc., leaves of successive ages.

smallest nearest the growing point, the oldest and most advanced farthest from it. A very short distance behind the growing point minute buds (*ax.b.*) are seen arising in the axils of

the young leaves and, as we get farther away from the apex, the former become more and more prominent until each is recognised as having the structure of the main bud in miniature. It will be noticed that the young leaves are closely crowded together and that the upper internodes are scarcely developed; consequently there is insufficient room for the enlarging leaf-blades which become thrown into numerous folds, and thus we obtain the familiar compact structure of a bud.

The Brussels Sprout is an example of a summer-bud in which the close packing gives sufficient protection to the young

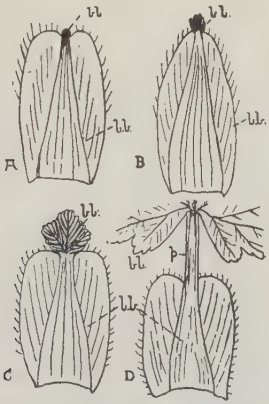


FIG. 50.—Transition between bud-scales and foliage-leaves in Flowering Currant; the successive stages are marked A–D and are all enlarged. *bl.*, blade; *l.b.*, leaf-base; *p*, petiole.

structures developing within, although even here the whole is enveloped in maturer leaves. In buds which have to withstand the rigour of winter additional protection is, however, necessary and this is provided in a number of different ways. Most commonly the bud is covered in by close-fitting leathery or membranous scales (the *bud-scales*), which are frequently brown (*e.g.* in Beech, Oak, Horse Chestnut), but sometimes black (*e.g.* in the Ash), and usually exhibit the same arrangement as the leaves upon the stem (*e.g.* the decussate scales of the Horse Chestnut, Fig. 48 D, and the alternate ones of the Lime, Fig. 48 C).

At first sight a bud-scale appears to differ very much from a foliage-leaf, but an examination of the opening buds of the Flowering Currant, for instance, will show that the one is but a modification of the other. If, starting at the outside, the bud-scales are removed in succession, a gradual transition will be found between them and the foliage-leaves within the bud (Fig. 50). The outermost scales are oval with a minute black apex (Fig. 50 A, *bl.*); a little further in, the scales show a somewhat larger tip which on careful scrutiny is seen to be a rudimentary or arrested leaf-blade (Fig. 50 B, *bl.*); still further in, the latter becomes more prominent (Fig. 50 C) and so by successive stages we come to the first foliage-leaves in which a petiole (Fig. 50 D, *p*) appears and in which the scaly enlargement at the base (*l.b.*) shows a diminution in size. In the innermost leaves of the bud this scale is seen to have contracted into a small leaf-base, such as we find in the mature foliage-leaves of the plant.

The transition just described shows plainly that the bud-scales of the Flowering Currant are nothing else than leaves with a much enlarged leaf-base and a more or less completely arrested lamina. The same sequence can be observed in the bud-scales of many other plants, such as the Sycamore, Ash, Horse Chestnut, etc. It is not always the leaf-base, however, that forms the bud-scale, for a study of the opening buds of the Beech (Fig. 51) or Elm will show that here the caducous stipules are the protecting structures. Whereas the inner scales are seen to arise in pairs from the bases of the unfolding leaves, a variable number of the outer scales, though likewise paired, have no corresponding blades. Just as in the buds of the Flowering Currant, therefore, the laminæ of the outermost leaves are arrested, only the part necessary for protection (in this case the stipules, in that the leaf-base) being represented.

Another type of bud-scale is seen in the Lilac and Privet in which, if the structures composing the bud are removed in succession and laid out in order, it will be found impossible to say exactly where to draw the line between bud-scale and foliage-leaf. In fact the bud-scales here are entire leaves of small size and leathery consistency. In the Willow the two bud-scales (Fig. 48 E) represent the first leaves of the shoot (p. 47).

Bud-scales are not always the only special protection of the winter-bud, for not uncommonly there is a layer of sticky varnish (*e.g.* Horse Chestnut, Poplar), which not only glues the scales together, but further reduces the risk of excessive transpiration (cf. pp. 9 and 16) from the young leaves within. Moreover, the latter are often equipped with numerous hairs, appearing as a white wool in the Horse Chestnut or as a dense brown

FIG. 51.—Photographs of Beech-twigs showing successive stages of bud-expansion. In the right-hand twig the stipular bud-scales can be seen adhering to some of the foliage-leaves. [Photo. E. J. S.]

covering in the Plane Tree and, as we shall learn later (p. 173), such hairs constitute a very efficient protection to the leaves. A few plants, of which the Wayfaring Tree (Fig. 48 A) and the Alder Buckthorn or Black Alder are the only British examples, rely solely on such a felt of hairs, their buds being naked without enveloping scales.

We may now again return to the study of the Brussels Sprout in order to follow up the stages in the development of the

foliage-leaf. If we remove some of the leaf-rudiments nearest the growing point, we shall find that, even with a lens, they appear as perfectly uniform structures, as yet showing no signs of the three parts of the mature leaf. Further back from the apex a distinction can be made between leaf-base and leaf-blade, both of which continue to expand so that the latter, as we saw above (p. 95), becomes much folded. It is only at a much later stage of development that growth takes place between the two regions resulting in the formation of the short petiole.

If we examine the buds of a number of different plants, we shall find that the way in which the young foliage-leaves are folded varies greatly (see Fig. 52, B–E). These folds often persist

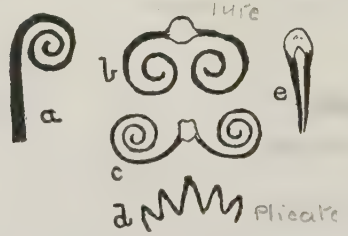


Fig. 52.—Diagram to explain method of folding of the young foliage-leaves; in all cases the blade is shown in section. A, Fern. B, Violet. C, Persicaria. D, Lady's Mantle. E, Laurel. In B–E the lower surface of the leaf is shown uppermost.

to some extent, for a brief period, after the leaf has emerged from the bud (*e.g.* Beech, Dock, Lady's Mantle, etc.), the young blade thus not exposing its full surface until the tissues have matured. An interesting case of such folding of the young lamina is seen in the Bracken and other Ferns in which, however, each leaf is separately protected and no proper bud is produced. Here both the main stalk and its branches (pinnæ) are spirally coiled, as in Fig. 52 A, the tender growing tip in every case being innermost; the latter is in this way adequately screened by the more mature outer portions of the blade, as well as by the numerous scales which cover it.

With the arrival of spring all the different parts within the bud begin to expand, the hitherto short internodes commence to lengthen out and the leaves to unfold, this taking place at the

expense of the food-materials which, as described on p. 16, are stored up in the woody branches. As a result the whole bud swells (Fig. 51), the bud-scales are forced apart, and the shoot begins to elongate. No lengthening out of the internodes, however, takes place between the bud-scales (except where they are stipules) which consequently remain as a crowded group at the base of the growing shoot. Sooner or later they drop off, leaving a number of broad flat scars which, on superficial observation, look like a series of closely set rings encircling the stem (see Fig. 40); since such *bud-scale scars* are necessarily formed only at the beginning of each season, the intervals between successive series mark as many years' growth of the branch.

The shoot is generally in an advanced state of development within the bud, in some early flowering plants (*e.g.* Lilac, Horse Chestnut, Flowering Currant) even including an inflorescence in which most of the parts are already present in miniature; the changes subsequent to opening are chiefly in the direction of a rapid increase in size of the different organs. Most of this growth, in the case of trees and shrubs, takes place in a few weeks, and during the remainder of the summer the buds (terminal and lateral) for the next year are being constructed. The enlargement of the shoot-system in a given season is therefore more or less dependent on the nature of the preceding one, and this applies especially to the extent of flowering in those plants in which the flowers are already formed in the winter-buds; of the latter many fruit-trees afford an excellent example.

Our study of the shoot would be incomplete without a discussion of the mechanical relations of its different parts. As in the Shepherd's-purse (p. 4, Fig. 1 C), the majority of Dicotyledonous plants have the hard woody strands arranged in a ring near the surface of the stem (*e.g.* the Bishop's-weed, Fig. 53 A) and around the soft inner tissue or *pith* (Fig. 1 C, *p*), which latter is occasionally replaced by a hollow canal (Fig. 53 A and Fig. 60 A). On the other hand, in Monocotyledons the strands are mostly scattered irregularly, though here also they are mainly collected towards the outside (*e.g.* in the Asparagus, Fig. 53 D). We have seen (p. 8) that these woody bundles also serve to transfer water from one part of the plant to another, but many stems contain other hard strands, the only use of which to the

plant lies in the added strength they afford it. These latter are often situated immediately beneath the surface-skin, giving a ribbed or fluted appearance to the stem (as in many members of the Parsnip-family, see Fig. 53 A of the Bishop's-weed), whilst in other cases (as in the Dead-nettle-family, see Fig. 53 B of the Hedge Woundwort) this strengthening tissue forms a continuous square tube in which the woody strands themselves are embedded.

By this superficial distribution of the harder substance a

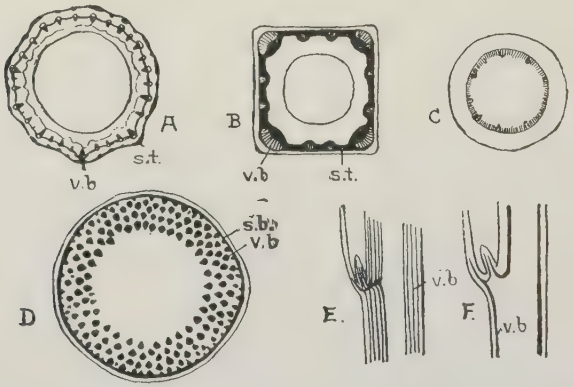


FIG. 53.—Diagrams of stem-structure. A–D, cross-sections (considerably enlarged). A, Bishop's-weed. B, Hedge Woundwort. C, Dicotyledon stem with continuous ring of wood. D, Asparagus. E–F, longitudinal sections through stem, leaf and axillary bud; E of Asparagus, F of Hedge Woundwort. *s.b.*, *s.t.*, non-vascular supporting tissue; *v.b.*, vascular strands.

maximum resistance to bending is combined with the greatest economy of material. For when a stem is bent, the tissue on the convex side is stretched out, whilst that on the concave side is pressed closer together, and the further we pass from the centre the greater will be the extension and compression respectively. From this we see that hard tissue placed right at the outside renders a stem best able to withstand bending; and since the strains to which a shoot is subjected, as a result of the force of wind and rain against the leaves, may operate in any direction, the advantage of an equal and symmetrical distribution of the strengthening tissue on all sides is obvious.

In contrast to the stem, the petioles of most leaves have to withstand a one-sided strain acting mainly from above and due to the weight of the blade, which may be much increased by wetting during rain. If we cut across such leaf-stalks, the hard strands will generally be found arranged in the form of an inverted arch, open on the upper side (see Fig. 54 A and C). This gives considerable strength to meet the usual bending strains from above, but is not so rigid as the closed tube found in stems and therefore allows of a certain flexibility which prevents the blade from being torn by sudden gusts. In such leaves as the Sycamore (Fig. 45), Wood-sorrel (Fig. 126), and Garden Nasturtium (Fig. 66 B), in which the petiole is attached more or less centrally and at right angles to the blade, the strain is almost equally distributed over the leaf-stalk and the

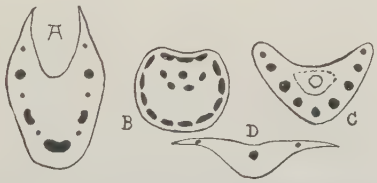


FIG. 54.—Diagrams of petiole-structure in cross-section (all considerably enlarged); vascular strands shown black. A, Comfrey. B, Sycamore. C, Bishop's-weed. D, Daisy.

arrangement of the hard strands is more like that of a stem (cf. Fig. 54 B). In radical leaves (*e.g.* Daisy, Fig. 54 D) which receive support from the ground on which they rest, the open arch arrangement is greatly flattened out.

Between the strands of the stem on the one hand and those of the leaf and its axillary bud on the other, there exists an intimate connection, readily seen if stems of Monocotyledonous (Fig. 53 E) or Dicotyledonous (Fig. 53 F) plants are halved lengthwise in such a way that the plane of halving passes through the insertion of a leaf. At the top of the petiole the strands pass over into the network formed by the veins, whereby the soft tissue of the blade is supported. The larger the lamina the greater the risk of being torn by wind or rain, and most large-leaved forms consequently exhibit a more or less extensive division of their foliage to form lobed or compound blades.

In woody Dicotyledons which year by year present a greater surface to the wind, the stem and its branches increase slowly in thickness by the addition of new layers of wood on the outside of that already formed (Fig. 53 C), so that the strength of the whole system keeps pace with the burden which it has to support. As the trunk of a tree becomes thickened in this way, the older and more centrally placed layers of the wood give up their water-conducting function and become modified to form the so-called *heart-wood* ; this is usually not only harder, but also darker in colour than the surrounding *sap-wood* and constitutes the part of the wood most used in the manufacture of furniture (*e.g.* Mahogany, Ebony).

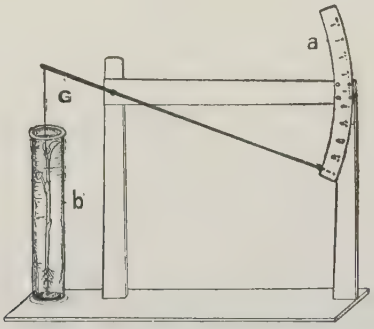


Fig. 55.—Apparatus to demonstrate shrinkage of an herbaceous plant due to loss of turgescence. Description of lettering in text.

The woody strands in the young shoots of trees and shrubs and in the stems of most herbs are by themselves insufficient to bear the strain, even of the plant's own weight. This is readily seen when plants in a vase droop for want of water, but again become erect when a fresh supply is added ; and the same observation can be made in nature on any hot summer's day. The obvious conclusion is that a proper supply of water is necessary for rigidity and, as a matter of fact, every living cell of a healthy plant is distended with liquid (*i.e.* it is *turgid*), so that it is as firm as an inflated cycle-tyre or a toy balloon.[1] The plant being largely composed of such turgid cells, the

[1] The turgid cells can readily be seen, if the cut surface of a Broad Bean stem is examined with a lens.

whole (*i.e.* root, stem and leaves alike) forms a stiff structure which only becomes flaccid when water is lost. Part of the liquid can be readily withdrawn from the turgid cells by placing herbaceous plants (*e.g.* any seedling) in a strong solution of salt for some minutes, when they become quite limp, though subsequent immersion in water restores the original turgidity (see Appendix VIII.).

An instructive experiment can be performed in this connection with the help of the apparatus shown in Fig. 55. It consists of a simple lever working over the surface of an arc (*a*), which is graduated (see Appendix IX.) to show the actual distance (*i.e.* amount of movement of the short arm G) to which the movement of the long arm of the lever corresponds. To the short arm G an entire herbaceous plant is firmly tied by its tip, whilst the root is attached to a weight sufficiently heavy (1–2 lb.) to keep the plant in position at the base of the gas-cylinder *b*, which should be tall enough to include the whole plant. If necessary, weights can be suspended from the long arm of the lever to keep the plant fully extended without undue strain. The cylinder is now carefully filled with strong salt solution and the position of the pointer on the graduated arc noted. After about half an hour the pointer will record a shrinkage of from a quarter to half an inch according to the plant used. If the salt solution is then siphoned off and replaced by water, the gradual recovery of the plant can be noted in the same way. From this we see that loss of water is accompanied by a decrease in size.

There is a further aspect of turgidity that plays an important part in the stability of the herbaceous plant. To study this point we select young shoots of the Elder (or in winter the flowering stems of Narcissus or Daffodil) and cut off a piece about 8 inches long with straight ends. The hard outer portion is then completely removed in four longitudinal strips leaving only the juicy central pith (p. 99) of the stem. If we now compare the length of the original piece with that of one of the outside strips and with that of the pith, we shall find that the former is a little shorter and the latter slightly longer. This indicates that in such a stem the pith is in a state of compression, whilst the outer tissues are in a state of tension. The advantage of this condition can be shown in the following way.

A weak spiral spring (such as can be made by twisting thin steel wire round a piece of wood), about 8 or 9 inches long, and a similar length of an inner tube of a cycle-tyre are obtained. Neither is capable of supporting itself in an erect position; if, however, the spring is slipped into the rubber tube and the former slightly compressed, so that the ends of the tube can be firmly tied, the two combined form a structure of considerable rigidity. Here, just as in the stem, the inner part is in a state of compression while the outer is extended.

It is in consequence of such tissue-tensions that many herbaceous shoots, when halved lengthwise, exhibit a curvature of the two halves with the exterior on the concave and the interior on the convex side; similarly the cut ends of the flowering stalks of Dandelions, when kept in water, split from

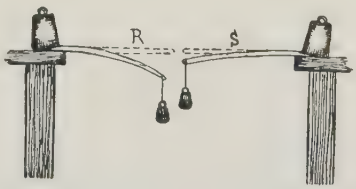


FIG. 56.—Method of demonstrating resistance to bending of root and stem. Description in text. *R*, root; *S*, stem.

below upwards into two or more portions, each coiling up like a watch-spring, with the inner side facing outwards.

In conclusion, the shoot may be briefly contrasted with the root. We have seen that these two parts of the plant differ essentially in the method of branching (p. 79), in the structures which they bear, and in the mode of protecting the growing tips (a root-cap in the root, a bud in the stem). Other differences lie in the colour, in the prevalent direction of growth, and in the functions which they perform. The mechanical construction of the root is also as a rule quite unlike that of the shoot, and each has been found to be suited to its particular needs. This point is best brought out by two simple experiments.

Selecting a herb or vigorous seedling, we cut off equal lengths of main stem and root; thin string is firmly bound round the two ends of each, and the pieces are then suspended from two nails. To the string at the other ends light scale-pans are

attached in which small weights in increasing amount are gently placed. It will be found that the root will support a greater weight or pull than the stem.

For the second experiment we use similar lengths of stem and root, which are arranged so that the greater part projects horizontally from the edge of a table, the small portion on the latter being held down firmly by a heavy weight, situated about a quarter of an inch from the edge (Fig. 56). Small equivalent weights are hung from the free end of each piece, whereupon it will be seen that the amount of downward curvature is much greater in the case of the root than in the stem, thus showing that the latter bends less readily than the former.

CHAPTER IX

The Plant in Relation to its Water-Supply

It was stated in the first chapter that the root-hairs are the organs by means of which water is absorbed from the soil,[1] but the way in which this is effected remains to be studied. It will help us in the first place to perform a simple experiment.

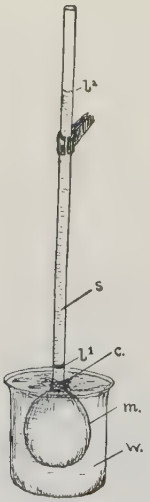


Fig. 57.—Demonstration of osmosis (Osterhout's method). *m*, egg-membrane; l^1, l^2, the successive levels of the sugar-solution. For other lettering, see text.

A small hole, about one-fifth of an inch across, is pierced through the pointed end of a number of eggs and the contents

[1] An experiment to prove that water is absorbed by roots was described in Chapter I. (p. 8).

blown out in the usual way (see Appendix X.). The shells are then placed singly in cups filled with a weak solution of vinegar in water ; this will gradually dissolve away the calcareous shell, leaving only the delicate membrane which lines its inner surface. A piece of glass tubing, about 8 inches long, is inserted through the hole in each membrane and the edge of the latter is bound tightly with cotton round the end of the tube (Fig. 57, *c*). The empty membrane is then completely filled with a strong sugar-solution (see Appendix XI.) till this rises about a quarter of an inch up the tube (Fig. 57, l^1). Thereupon the whole is fixed

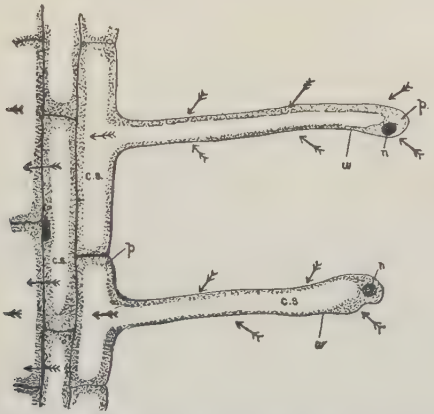


Fig. 58.—Diagram of surface-cells of root with two root-hairs (very considerably magnified). The direction taken by the water is indicated by arrows. *c.s.*, cell-sap ; *n*, nucleus ; *p*, protoplasm ; *w*, cell-wall.

in such a way that the membrane (*m*) is completely immersed in a tumbler of water (*w*), and the level of the sugar-solution marked by a strip of gummed paper (l^1). After a short time the liquid in the tube will be found to have risen, and this continues till ultimately the whole tube is nearly full (l^2). Occasionally the membrane leaks, and therefore it is advisable to set up several experiments.

We can conclude from the foregoing result that water has passed through the membrane into the sugar-solution and has thus brought about the change in level observed. If we could substitute for the egg-membrane and sugar-solution a root-

hair or other living cell of a plant, either of which contains a strong-solution (the *cell-sap*) analogous to that of the sugar, we should obtain the same result. Indeed, wherever two solutions of different strengths are separated by a suitable vegetable or animal membrane, the weaker gives up water to the stronger, a process which is known as *osmosis*. In the case of the root-hair we have a weak solution, the soil-water, and a relatively strong one, the cell-sap (Fig. 58 *c.s.*), separated by such a membrane which is here constituted by the cell-wall (Fig. 58, *w*) and the living substance or *protoplasm* (*p*) lining the inner surface of the latter; in the protoplasm a denser body, the *nucleus* (*n*), is seen.[1]

The soil-water is therefore continually being drawn into the root-hairs and, as moisture is thus absorbed, further water flows in from the surrounding soil to take its place; the cell-sap of the root-hair thus becomes diluted (*i.e.* weaker than that of the cells lying beneath the surface-skin), so that the water will begin to flow inwards by osmosis (see the arrows in Fig. 58). In this way it gradually moves towards the centre of the root and thus ultimately reaches the woody strand, whence it passes to the stem and leaves. It may be added that the exact way in which the transference to the wood takes place is not yet fully understood.

The structure (viz. cell-wall, protoplasm, nucleus, and cell-sap) just described for the root-hair is exhibited with minor modifications by every living cell, but in the mature condition many of the component elements of the plant's body are dead (*e.g.* the vessels described on p. 111 and many of the supporting elements considered in the last chapter). The turgid character of the living cells (p. 102), when in a healthy condition, is due to the attraction of water into the cell-sap which thus distends the cell-wall and underlying protoplasm to their utmost limit. This can be illustrated by filling an egg-membrane, obtained as above, with strong sugar-solution (see Appendix XI.) and, after securely tying up the opening, placing it in a vessel of water. The membrane, which at first is flabby, gradually becomes more and more distended as water is taken up, *i.e.* it becomes firm and turgid.

[1] These details of the structure of a root-hair are only apparent under a microscope.

Returning to the absorption of moisture by the root, we have first to notice that under certain circumstances the water appears to be pumped into the wood with great vigour, so that a considerable upward pressure (so-called *root-pressure*) is manifest. This may be demonstrated in the following way (Fig. 59): The stem of a plant of the Fuchsia or Vegetable Marrow growing in a pot is cut off about 2 inches above the level of the soil. To the cut stump a piece of glass tubing (about a yard long) is firmly connected by a short length of rubber tube, both joints being wired on (see Appendix VII. and Fig. 59). A

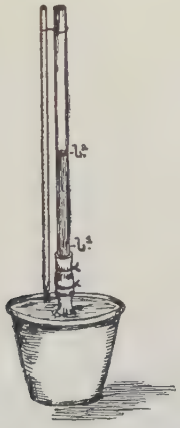


Fig. 59.—Demonstration of root-pressure, see text. l^1, l^2, the successive levels of the water-column.

little water is now poured into the tube (see Appendix XI.) and covered with a drop of oil to prevent evaporation, after which the level (l^1) is marked in the usual way. The soil is well watered and the whole is kept in a warm place. Very soon the liquid in the tube will begin to rise and, in the case of a sturdy plant, will not take long to reach the top.

It will be obvious that, when such root-pressure exists, it must help in forcing water up the stem, particularly when the latter is of no considerable height; an effective root-pressure is, however, in nature realised only at certain times (mainly in spring). Such pressure also finds expression in another way, viz. in the phenomenon of *bleeding*, in which the exuded

liquid collects on the cut end of the stem, as is well seen in the Cress and in the Grape Vine.

We have already shown (p. 8) that the woody strands are the channels through which the water passes, but a further proof is supplied by the fact that a ringed branch (*i.e.* one from which all the tissues outside the wood have been removed for a short distance) remains healthy for weeks, if left on the plant or kept in water under suitable conditions. In such a case the

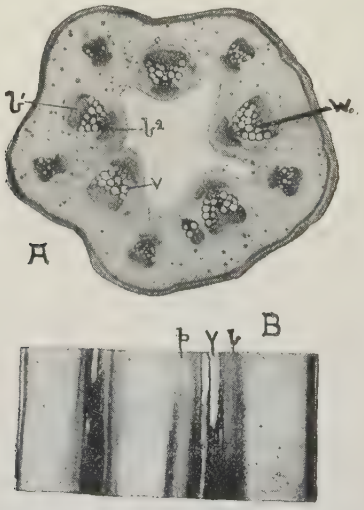


FIG. 60.—A, Cross-section, and B, Longitudinal section through stem of Vegetable Marrow. (Photomicrographs, both enlarged about 3 times.) b^1, outer bast ; b^2, inner bast ; *p*, pith ; *v*, vessel ; *w*, wood.

moisture can be travelling only through the wood or the central pith, but since the latter completely disappears from the mature stem of many plants (p. 99), it is obviously not essential for water-conduction.

In order to study the structure of the woody strands through which the water travels, we may repeat the experiment of placing a plant in a solution of red ink, as described on p. 8, in this case, however, using a sturdy seedling of the Vegetable Marrow. When the coloured liquid has reached the leaves, the different organs should be cut across and examined with

a lens; or a better method is to cut thin slices of each with a sharp pocket-knife or razor and place these in a layer of dilute glycerine between two small sheets of thin glass (*e.g.* photographic plates from which the film has been removed), when by holding them up to the light the structure can be much more readily seen. In the coloured woody strands, whose distribution we have already noticed (p. 99), a number of large circular cavities surrounded by a thick wall will be observed (Fig. 60 A, *v*). If now longitudinal sections are prepared in the same way, these structures will again be seen as long narrow tubes, with a thick wall, running lengthwise through the strands (Fig. 60 B, *v*). These tubes or *vessels*, as they are called, are the chief channels through which the water travels and will be found alike in all parts, constituting, together with other purely supporting elements, the woody strands of the plant.

That these vessels actually serve to convey the water can be shown as follows: Place the cut end of a healthy shoot for some minutes in butter, which is kept melted, and then put it aside to cool, so that the butter sucked up into the vessels solidifies. The extreme end having been shaved off, the shoot together with another not thus treated is placed in water. After some hours, whilst the latter is still fresh, the former has faded owing to the plugging up of its vessels.

We have learnt in the last chapter (p. 102) that woody perennials exhibit an annual increase of the wood, serving to provide additional support to the constantly expanding crown. The annual increments, however, not only fulfil this purpose by providing extra supporting tissue, but also contain new vessels and, according to the relative amounts of the two, the wood is 'soft' or 'hard.'

In Dicotyledonous tree-trunks, which have been cut across, the vessels (Fig. 61 A, *v*) look like small pin-pricks on the smooth surface of the wood. Since the greatest demand for water is made in the spring, when the new leaves unfold, the wood formed at this time in each year is rich in vessels (*spring-wood*, Fig. 61 A and B, *S.W.*), whilst that produced later, when the water-requirements are satisfied, consists mainly of supporting tissue (*autumn-wood*, Fig. 61 A and B, *A.W.*). This difference leads to the formation of the *annual rings*, which can be seen in any cross-section of a piece of wood and which are due

to the sharp boundary between the autumn-wood of one year and the spring-wood of the next. Traversing such a cross-section like the spokes of a wheel are a number of lighter-coloured streaks the so-called *medullary rays* (Fig. 61 A, *m.r.*); all of these start at the outer edge of the wood but, whereas some extend right up to the central pith, others die out at

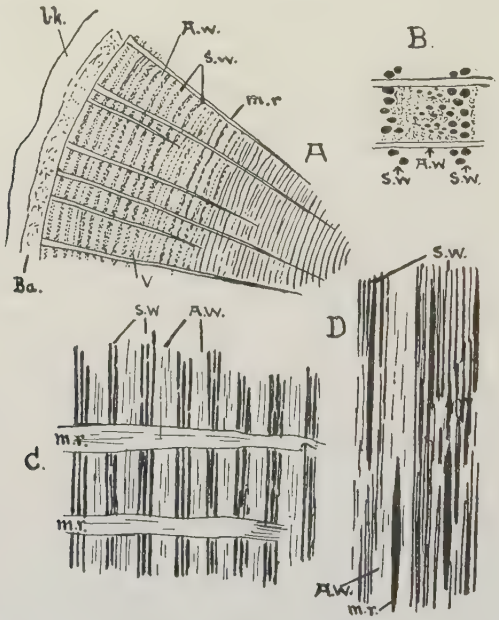


FIG. 61.—Structure of a woody trunk (somewhat enlarged). A, Portion of a cross-section. B, Small part of wood of same, more enlarged. C, Radial longitudinal section of the wood. D, Tangential longitudinal section of wood. *A.W.*, autumn-wood ; *Ba*, bast ; *bk*, bark ; *m.r.*, medullary rays ; *S.W.*, spring-wood ; *V*, vessels.

varying distances from the edge. To complete our description we may notice that in the tissue on the outside of the wood two layers can generally be recognised ; close to the wood we have the looser *bast* (Fig. 61 A, *Ba.*), whilst the surface is constituted by the relatively compact *bark* (*bk.*).

If we examine a block of wood which has been cut lengthwise through the centre (*i.e.* radially, Fig. 61 C), we can recognise

the long tubes formed by the vessels (*S.W.*) and irregularly shaped silvery bands passing across them (the silver grain of the Oak), which represent the medullary rays (*m.r.*). When the wood is cut lengthwise near the outside (*i.e.* tangentially, Fig. 61 D), the same features can be made out, the medullary rays (*m.r.*) now, however, appearing as short vertical streaks.

Certain differences are observed in cross-sections of the woody stems of Conifers (*e.g.* Spruce Fir, Scotch Fir, etc.). In

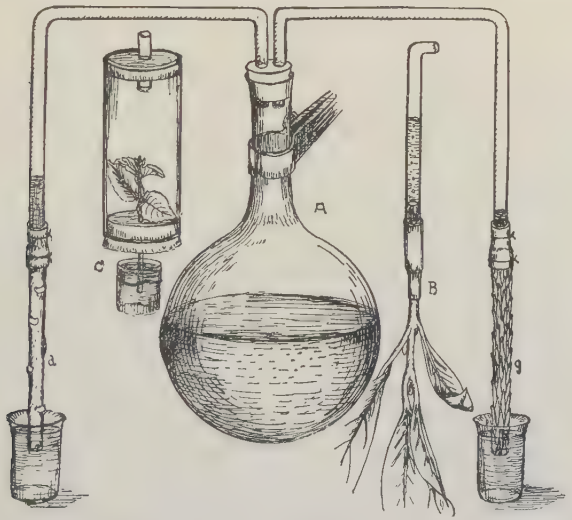


FIG. 62.—A, Apparatus for comparing the rate of flow of water through the wood of two shoots (*d*, Elm ; *g*, Conifer). B, Modification of same apparatus to show that there are apertures in the leaf through which gases can pass in and out. C, Modification to be used for the demonstration of water-pores. For details, see text.

the first place, the wood is noticed to be remarkably uniform, in fact it consists only of one kind of element, serving both for mechanical support and for conduction of water. These elements are much narrower and shorter than the vessels of Dicotyledonous plants, but differences in size and the thickness of the walls between those formed in spring and autumn give rise to similar annual rings. The absence of special mechanical tissue renders the wood easy to work and is responsible for the term soft wood, in contrast to the hard wood of Dicotyledons.

The rate of flow of the water through the wood varies greatly from plant to plant and, for instance, is appreciably less in the case of a Coniferous than in most Dicotyledonous stems, a fact which can be shown in the following way (Fig. 62 A): A round-bottomed flask is provided with a two-holed rubber cork, through each hole of which a piece of glass tubing twice bent at right angles is inserted (as in the figure). The one arm of each glass tube should project only for a short distance below the cork, while the other free arm should be considerably longer. To the open end of the latter a short piece of stem (in the one case of a Conifer (*g*), in the other of an Elm (*d*), both being of equal length) is fitted by rubber tubing, so as to make an air-tight connection (see Appendix VII.). Each piece of stem should be previously coated, all except its two ends, with a layer of melted paraffin-wax, so as to close up all apertures and scars. The rubber cork with attached tubing is now taken out of the flask and the latter is half filled with water which is heated until it has boiled for a minute or two. Whilst vapour still fills the flask, the rubber stopper is fitted into it, after which the flask is placed in a vessel of cold water, the unattached ends of the two stems being allowed to dip into tumblers of water (Fig. 62 A). The reduced pressure within the flask, resulting from the condensation of the contained aqueous vapour, leads to a strong suction and as a result columns of water which have traversed the two stems will form in the tubes above their upper ends, the height of each being proportional to the rate of flow (Fig. 62 A).

Through the vessels in the woody strands the water ultimately flows into the leaves and from these, as we have already seen (p. 9), a great part is given off in the process of *transpiration*. The cobalt-method described on p. 9 will serve to show the occurrence of transpiration from any leaf. Another familiar demonstration is the collection of moisture on the inside of a bell-jar placed over a healthy plant, although in order to obtain a reliable result both pot and soil should be covered with some water-proof material (*e.g.* silver paper).

It was noticed in applying the cobalt-method to the Shepherd's-purse (p. 9) that transpiration was more rapid on the lower than on the upper side of the blade, and this would be found to be the case in very many (*e.g.* Lilac, Vine, Black Pop-

lar), though not in all plants. Choosing two healthy leaves of the normal type, the ends of the petioles, and in one the lower surface of the blade as well, are covered with vaseline, after which the two are hung up in a warm room. A few hours later the unvaselined blade will be more or less withered, whilst the other will have remained almost fresh. This again indicates that transpiration is most active on the lower surface, for the effect of vaselining the latter is to close up the pores mentioned on p. 9, through which the water-vapour chiefly escapes. We may now verify the existence of such apertures connecting the interior of the leaf with the outside atmosphere.

For this purpose we employ the same apparatus (Fig. 62 A) as was described on p. 114, using two similar leafy shoots (or leaves) in which the cobalt-test has shown transpiration to be much more active from the lower side. In the one the under surfaces, in the other the upper surfaces of the blades are vaselined, after which the shoots (or petioles) are attached to the free ends of the glass tubes (in the way shown in Fig. 62 B), so that the cut end of the former extends into the latter above the level of the surrounding rubber. Prior to doing this the long arm of each tube is partially filled with a column of water extending some 4 to 6 inches above the end of the stem (or petiole). Proceeding as before (but dispensing with the tumblers of water), we find that when the flask is cooled a stream of air-bubbles begins to arise from the cut end of the shoot (or petiole), in which the upper sides of the blades had been vaselined, and to ascend through the column of water in the long arm of the tube; this may go on for several hours as the flask becomes cooler. From the other stem (or petiole), however, few or no bubbles arise. This indicates that, in leaves in which transpiration takes place mainly from the lower surface, the openings through which air can pass into the interior of the plant are also practically confined to that side. Incidentally this experiment also shows that the plant is traversed by a continuous system of air-spaces opening to the exterior by the pores in the surface-skin.

The actual pores can be located by sealing up the cut end of the petiole with melted paraffin-wax and immersing the blade in warm water, when owing to the expansion of the air in the leaf the lower surface will become studded with numerous tiny

air-bubbles, each marking the position of a pore. If we strip off a piece of the surface-skin from the lower side of the lamina of a White Lily, place it in water between two sheets of thin glass and, holding it up to the light, examine it with a good lens, the pores can be distinguished as dark lines traversingthe long axis of small elliptical areas (the *stomates*, Fig. 63 A, *s*). Each such stomate (Fig. 63 B) consists of two sausage-shaped cells

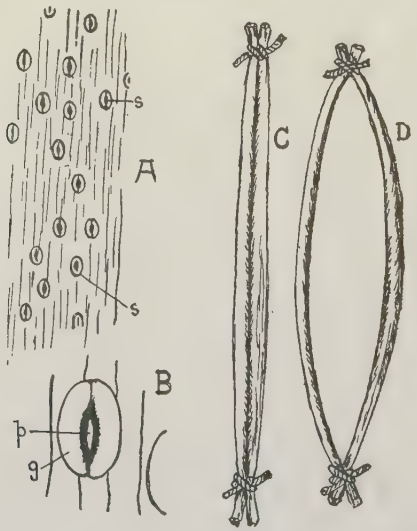


FIG. 63.—A, Surface-skin from leaf of White Lily, showing stomates (*s*) (somewhat magnified). B, A single stomate (very considerably enlarged). *p*, pore; *g*, one of the two bounding cells. C, Artificial stomate, closed. D, The same, open. For details, see the text.

(*g*) surrounding the slit-shaped pore (*p*), which appears dark owing to its being occupied by air (see also Fig. 68 B, *St.*).

Comparison of fresh and faded leaves of the same plant with the help of the cobalt-method indicates that transpiration is greatly reduced in the wilted ones (p. 10), which is due to a marked decrease in the width of the pores. Such a diminution in width takes place whenever the two cells bounding the pore become less turgid through excessive transpiration. In this way the plant is able to regulate the amount of evaporation

from its surface in correspondence with the supply of moisture, since at all other points the escape of water-vapour is more or less prevented by an impermeable covering, the *cuticle* (see Chapter XIII., p. 171).

A rough model of a stomate may be made in the following way (Fig. 63 C and D) : A straight piece of the flower-bearing stalk of a Jonquil or the internode of a Dog's-mercury, about 3 to 4 inches long, is halved lengthwise, the two halves being then placed in a strong solution of salt until they become flaccid (p. 103). They are thereupon placed parallel to one another with the original outer surfaces in contact, while what was previously the inner surface is directed outwards. In this position the two halves are firmly tied together by string at their two ends (Fig. 63 C). If the two pieces thus joined are placed in water, they will in the space of a few minutes, as they again become turgid, arch apart so as to leave a wide aperture between them (Fig. 63 D)—in other words, the pore of our artificial stoma opens. A return to the salt-solution will once more result in a closure, and this sequence of events can be repeated several times.

If the artificial stoma, with the pore widely open, is for some time allowed to dry slowly by exposure to the air, a marked decrease in the width of the opening becomes apparent. The opening and closing of this model is due to the greater extensibility of the side away from the pore (cf. p. 103), and we may add that a difference in stretching power between the two sides of the cells bounding the aperture of a true stomate is there too in part responsible for its change in size (see Appendix XXIV.).

We have hitherto only described methods of demonstrating transpiration, but in some cases it is advisable to measure the rate of this process and for this purpose an instrument known as a *potometer* is used. The shoots employed in experiments with this instrument should be removed from the plant some hours previously and kept in water; before use the lower 3 inches of the stem should be cut off previous to removal from the water. The potometer (Fig. 64) consists of a 2 oz. bottle with a wide neck, fitted with a three-holed rubber cork into the holes of which we insert respectively : (i) a cylindrical funnel (*a*) passing into a narrow glass tube provided with a stopcock (*b*) ; (ii) a piece of capillary tubing (*c*) bent once at right angles and with a scale attached to the horizontal arm ; (iii) a piece of

ordinary glass tubing (*d*) bent as shown in the figure. To prepare the instrument for use the stopcock is opened and water is poured into the funnel until it overflows from the ends of tubes *c* and *d*, whereupon *b* is closed.

A short length of rubber tubing is carefully passed over the end of a leafy shoot (see Appendix XII.), and by this means the latter (*e*) is attached to the glass tube *d*, so that the end of the stem dips into the water; the connection is rendered air-tight by binding the rubber onto stem and tube respectively with wire. If the horizontal arm of the capillary tube *c* is carefully

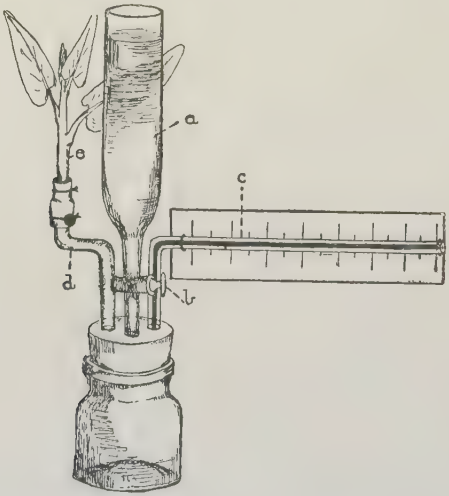


FIG. 64.—Potometer (Farmer's method). Full description in text.

watched, a column of air, starting at the open end, will be seen to creep along it; this is due to the fact that the moisture lost in transpiration from the leaves is replaced by an almost equal amount taken up from the bottle. By opening the stopcock, until the column of air has been driven back, and again closing it, the potometer is prepared for a fresh observation; and, if we record (with the help of the seconds-hand of a watch) the time taken for the end of the air-column to pass over a measured distance on the scale, the average of several readings will give an estimate of the rate of transpiration from the shoot employed.

In this way we can determine and compare the rates of transpiration[1] from shoots of different plants, the contrast afforded by evergreen and deciduous types being specially instructive. Moreover we can use the potometer to study various aspects of transpiration. If, for instance, half the leaves of a shoot are removed or vaselined, it will be found that, as a result of the reduced transpiring surface, the rate of absorption (as indicated by the movement of the air-column) is in either case much decreased. We may also compare shoots exposed to different conditions, such as a hot and a cold room, dry and moist air, moving air (*e.g.* a draught) and still air, and in each case we shall find that the first of the two alternatives induces more active transpiration. This process is therefore accelerated by heat, dryness of the air and wind.

The actual amount of transpiration in a given time can be measured by placing a potted plant (soil and pot being covered with waterproof material) on one scale-pan of a coarse balance and putting sufficient weights on the other to counterbalance it. After some time the scale-pan bearing the plant will be found to have risen, and by adding weights to it the amount lost in transpiration can be gauged. If a perfectly accurate result was required, it would be necessary to allow for the gain in weight as a result of assimilation and the loss due to respiration (cf. p. 187).

A somewhat more accurate method is to place the plant (soil and pot again being covered), together with a weighed amount of dry calcium chloride (which eagerly absorbs moisture), underneath a bell-jar, whose lower edge is greased so as to make an airtight joint with the glass plate on which it rests. A control should be fitted up with an equal amount of calcium chloride, but with a pot having no plant. If after some time the two lots of chloride be reweighed, that from the bell-jar containing the plant will be found to be much heavier, and the difference between their weights will give the amount of water-vapour transpired.

As a result of the giving off of moisture from the surface of the plant in transpiration, a marked suction is produced, which can be readily demonstrated by the experiment shown in

[1] In reality of course the potometer measures the rate of absorption; but we may take it that this is proportional to the rate of transpiration.

Fig. 65 A. The end of a leafy shoot (cut under water, see p. 117, and with the surface of the stem vaselined) is firmly fixed by rubber tubing into the upper end of a long narrow glass tube filled with water (see Appendix XI.), the lower end of the tube dipping into a vessel containing mercury (or lubricating oil). By slow degrees the mercury (or oil) will be seen to rise in the tube, replacing the water sucked up by the shoot as a result of its transpiration. That this is a purely physical phenomenon can be shown by substituting some porous mass for the shoot. The bulb of a thistle funnel is *loosely* packed with wet Plaster of Paris (*p* in Fig. 65 B), which in setting will expand sufficiently to fill it

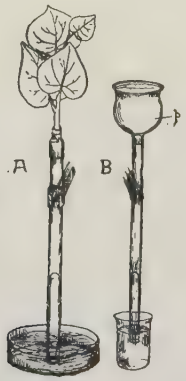


Fig. 65.—A, Demonstration of suction due to transpiration. B, Demonstration of suction due to evaporation from a porous mass (*p*). For details, see text.

completely. The stem of the thistle funnel is then filled with water and its lower end placed as before in mercury or oil, when a similar gradual rise of the latter is observed. Experiments of this kind, carefully performed, have shown that the mercury will ascend to a considerably higher level than that supported by ordinary atmospheric pressure (viz. 30 inches).

It will be obvious that this suction must materially assist in the upward passage of water through the plant, but the entire mechanism of the ascent of sap is far from being properly understood and involves such complicated principles that its consideration would be out of place in a book of this scope. When a plant is obtaining abundant moisture, so that absorp-

tion is in excess of transpiration (and it is at such times that root-pressure is generally to be observed), the water in the vessels is forced upwards under a positive pressure. As soon, however, as transpiration is only just balanced by absorption, the water in the vessels is being pulled up by suction, so that it is in a state of tension. Under these circumstances the pressure of the water in the vessels is less than that of the atmosphere, *i.e.* we have a *negative pressure* which can be demonstrated as follows.

If the stem of a plant, which has recently been little watered, is cut across and water placed on the exposed surface of the stump, it will be eagerly sucked up. When the stem of such a plant is cut open under a solution of red ink, the red liquid, on splitting up the stem, will be found to have penetrated into the vessels to a much greater distance than in the case of a plant which has been well watered.

It is a familiar fact that if plants are gathered on a hot summer's day, when a negative pressure is almost invariably realised, they often wither even though placed in water soon after. This is due to air being sucked up into the vessels which consequently lose their power of conducting moisture. If two shoots are cut, one under water and the other in the air, from a plant in which negative pressure has been demonstrated, the two being afterwards placed in water, the former will remain fresh, whilst the latter soon fades. Hence the necessity of cutting shoots under water, if they are subsequently to be used for transpiration-experiments (cf. p. 117).

At certain times, when abundant absorption results in a considerable positive pressure, the excess of moisture cannot be altogether removed by transpiration and in many plants escapes through special apertures (the *water-pores*), over which it frequently collects as small drops of liquid. These are usually situated on the margins of the leaves, *e.g.* at the ends of the principal veins of the peltate blade of the Garden Nasturtium (Fig. 66 B), at the tip of the leaf in Grasses (Fig. 66 A), or upon the leaf-teeth in the Marsh Marigold and Fuchsia. If any one of these plants, in a well-watered condition, is placed beneath a bell-jar in a warm moist atmosphere, the drops of liquid marking the positions of the pores soon appear.

They can be demonstrated more rapidly with the help of

the apparatus illustrated on p. 113, using, however, but a single glass tube to the end of which is attached a short and wide cylinder, as in Fig. 62 C. A branch is tightly inserted through the hole in the lower cork (see Appendix XII.), so that its foliage is situated within the cylinder, whilst its cut end projects below into a vessel containing water. Owing to the reduced pressure produced within the flask, as in previous experiments, a considerable quantity of water is sucked up into the shoot, and drops of liquid soon form over the water-pores.

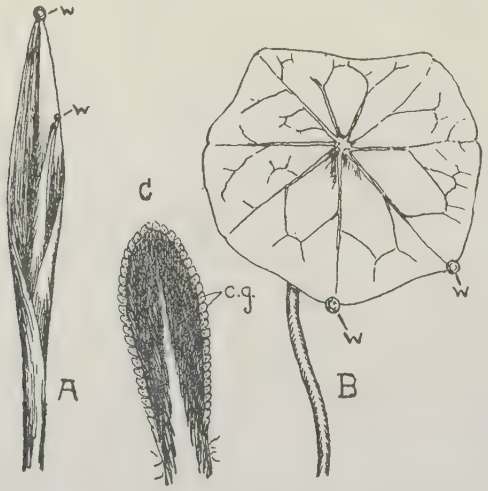


FIG. 66.—Leaves with water-pores. A, Maize. B, Garden Nasturtium (peltate leaf). C, Saxifrage with chalk-glands (*c.g.*). *W*, the drops of water above the water-pores.

The water passed out through these apertures is not pure, but contains various substances in solution. In some cases the amount of dissolved material is so considerable that, as the liquid evaporates, a deposit accumulates above the water-pore, as is well seen in the so-called chalk-glands of many Saxifrages (Fig. 66 C, *c.g.*).

The details given in this chapter will have made it clear that plants absorb a far larger amount of moisture than they directly need, since most of it is given off again in the process of transpiration. It is, however, essential that as much water

as possible should pass through the plant, in order that sufficient mineral salts from the dilute solution may accumulate in its leaves for a rapid manufacture of the necessary food-materials; and it is only if transpiration is abundant that this end can be attained. Apart from this, transpiration is also useful, because it tends to lower the temperature of the leaves which, particularly on hot sunny days, run a risk of being overheated.

CHAPTER X

The Nutritive Process of the Plant

The water, whose course we have now fully traced, contains various mineral salts in solution (cf. p. 9) which help in one way or another to build up the body of the plant. But we have also seen that part of the water itself is retained and this is employed for diverse purposes, viz. (i) in combination with the carbon dioxide of the air to form the starting-point of the organic substance of the plant, (ii) to keep the cells in a turgid condition (cf. pp. 102 and 108), (iii) to serve as a medium for transference of soluble materials from one part to another, and (iv) to permeate the cell-walls and protoplasm. Uncombined water thus constitutes a great part of the plant's body, as can be readily seen by comparing the weight of a fresh and a dried plant.

To ensure a more accurate comparison a considerable quantity (*e.g.* about 100 grams) of fresh material is cut up into small pieces, put into an evaporating dish of known weight, and the two weighed together. The dish is now placed over a water-bath (Appendix VI.) and heated for at least twenty-four hours. After cooling it is reweighed, the weight is noted and then the dish is again heated; this is repeated until two successive estimations give the same result. The weight of the evaporating dish having been subtracted in each case, it will be found that the final weight of the material is far less than the original one. Since the temperature of the water-bath would be only sufficient to drive off the uncombined water, the loss of weight recorded corresponds to the amount of the latter; the weight of the remaining substance is consequently known as the *dry weight* and is usually expressed in percentages of the fresh weight.

The dry weight varies considerably according to the kind of plant or the portion of it used; thus, in a woody plant it

amounts to about 50 per cent., in an herbaceous plant to about 30 per cent., and in a water-plant (as well as in many edible fruits) to little more than 5 per cent. We therefore see that, in all but woody plants, the uncombined water constitutes the major part of the plant's substance. This does not, however, apply to dormant seeds in which the dry weight usually represents about seven-eighths of the total, and we can consequently understand why, as a preliminary to germination, so large an amount of moisture has to be absorbed (cf. p. 26).

In order to study further the composition of the plant we place the dried material, obtained as before, in a weighed crucible and heat it strongly for several hours over a Bunsen burner. The mass first becomes charred (but the temperature should not be so high as to cause it to glow) and then gradually assumes a greyish-white colour like that of tobacco-ash. During this heating process all the Carbon, Hydrogen, Oxygen, and Nitrogen compounds composing the plant are broken down and escape, chiefly in the form of various simple gases (*e.g.* carbon dioxide, water-vapour, free nitrogen, etc.), and the matter that remains (the so-called *ash*) consists of the mineral constituents of the plant (*e.g.* silica, potassium carbonate, etc.).

If, after cooling, the weight of the ash is ascertained, it will be found to represent but a small fraction of the original dry weight (*e.g.* about 4 per cent. in a Potato, about 7 per cent. in the Clover, and as much as 17 per cent. in Tobacco-leaves). In order to obtain a fairly accurate estimate of the ash the heating must be repeated, as in the case of the dry-weight determination, until no further decrease takes place. Analysis of the ash (Appendix XIII.) of a large number of plants has shown that it always contains compounds of the following elements, though varying considerably in their relative amounts: Aluminium, Calcium, Chlorine, Iron, Magnesium, Phosphorus, Potassium, Silicon, Sodium, Sulphur. To these we must add the elements Carbon, Hydrogen, Nitrogen and Oxygen, which were present in the dried material before its conversion into ash, so that compounds of fourteen chemical elements are practically always to be found in the plant. Not all of these are, however, really essential, as can be shown by growing plants in so-called *water-cultures*.

For the setting up of water-cultures (Fig. 67, see also Ap-

pendix XIV.) we require a number of large jars, the interiors of which are sterilised (*i.e.* rendered free from germs) by first rinsing them out thoroughly with commercial nitric acid and then washing out the latter with boiled water, until it gives no indication of an acid reaction with litmus. The sides of the jars are then covered with black paper in order to exclude light, and each is fitted with a cork pierced by three holes; through two of these a short length of glass tubing is inserted, whilst the middle one is left open to receive the plant. One jar is now

FIG. 67.—Water-culture.

filled about four-fifths full of distilled water, whilst a second receives a culture-solution made up as follows :—

Potassium nitrate	1 gram.
Magnesium sulphate	1 gram.
Potassium phosphate	1 gram.
Calcium nitrate	4 grams.

The first three are dissolved in two litres (*i.e.* about $1\frac{3}{4}$ quarts) of distilled water, whereupon the fourth is added, as well as one or two drops of iron chloride; after this the solution is boiled for about half an hour, any diminution in volume being made good with distilled water. Some precipitate is generally formed, but this is later dissolved by the roots of the plant.

A young seedling (preferably, if a rapid result be desired, of some plant with scanty food-reserves in its seeds) is now inserted through the middle hole of the cork in each jar, so that its roots just dip into the water, the plant being kept in position by packing it round with cotton-wool. The glass tubes, whose upper ends are closed with plugs of cotton-wool, serve for the daily aeration of the liquid in the jar and also for the addition of fresh distilled water, when necessary (see Appendix XV.).

After some weeks the plant growing in distilled water will have a starved and stunted appearance, whilst the other one is flourishing; this shows that the compounds in the culture-solution are sufficient for its growth, whereas water alone is inadequate.[1] If now culture-solutions are prepared, each lacking *one* of the elements in the above formula (Appendix XVI.), it can be proved that each is necessary for healthy growth. Thus, if Nitrogen be absent (which can be effected by substituting Potassium sulphate for Potassium nitrate and Calcium chloride for Calcium nitrate in the culture-solution), the seedlings fail to reach any considerable size and sooner or later die. This shows that the great volume of free Nitrogen in the atmosphere cannot be used directly by the ordinary plant (regarding the exceptional behaviour of members of the Pea-family, see p. 147).

The living part or protoplasm of the plant is invariably composed of Carbon, Hydrogen, Oxygen, Nitrogen, Sulphur and Phosphorus, so that in the absence of a suitable supply of Nitrogen no protoplasm can be formed and growth is impossible after the food-reserves in the seed are exhausted; for a similar reason, if Sulphur or Phosphorus be lacking in the culture-solution, no appreciable growth can take place. The elements Calcium, Potassium and Magnesium appear to play some important part in the building up of protoplasm, although they need not necessarily enter into its final composition. Iron is required for the formation of chlorophyll and, when compounds of this element are altogether absent (which is difficult to secure owing to the presence of Iron as an impurity in most chemicals), the leaves become cream-coloured and are said to be *chlorotic*.

Our experiments with water-cultures therefore show that

[1] Both plants can of course obtain Carbon in the ordinary way from the carbon dioxide of the atmosphere.

the following nine elements are essential for the nourishment of the plant: Calcium, Hydrogen, Iron, Magnesium, Nitrogen, Oxygen, Phosphorus, Potassium and Sulphur; to these we must add Carbon which was proved to be necessary in the first chapter (p. 11). All of these, with the exception of Carbon, are obtained from the soil in the form of simple soluble inorganic compounds like those used to make up the culture-solution. Some of the minerals in the soil are, however, only slightly soluble in water, but the carbon dioxide given off from the surface of the root-hairs in respiration (p. 12) unites with the soil-water to form carbonic acid; this has considerable solvent powers, and thus the plant itself brings into solution some of the compounds which it requires.

This corrosive action of the root-hairs can be demonstrated by planting seeds in soil just above a piece of polished marble (or the inner surface of a mussel-shell), when after about a fortnight the surface will be seen to have become etched, where it is in contact with the roots.

A striking feature of the absorptive process is that different kinds of plants growing side by side in the same soil take up some compounds in very diverse amounts. Thus, the ash of Grasses consists largely of silica (to which the hard surface is due), whilst that of other meadow-plants contains but little. Similarly Seaweeds contain so much Iodine, that until relatively recent times their ash formed the principal source of this element, although it is only present in sea-water in exceedingly minute quantities.

It will be noticed that the complete water-culture solution in which the plant thrived contained no Carbon-compound, and indeed it is impossible to replace the carbon dioxide of the atmosphere in any way. This can be proved by growing a plant in a normal culture-solution, with the apparatus shown in Fig. 5 (p. 11), and noting the subsequent absence of starch in the leaves as compared with a control;[1] the addition of carbonates or other Carbon-compounds to the solution makes no difference to the result. The carbon dioxide, which is thus indispensable to the

[1] An improvement on the method described and figured on p. 11 is to use a bell-jar having an opening at the top, which is fitted with a cork holding a U-tube also filled with soda-lime. In this way the plant receives a better supply of air.

formation of starch in green leaves, is found only in small amount in the atmosphere (about three parts in 10,000 of air) and obtains access through the stomates (p. 116). For, if the under sides of the leaves of a Lilac-shoot be covered with vaseline, the shoot having previously been kept in the dark until all the starch has disappeared, none will be formed on exposure to light. On the other hand, a control shoot with unvaselined leaves, but otherwise similarly treated, gives the starch-reaction (p. 10) after a short time.

By cutting across the blade of a Privet, Cherry Laurel, or Holly (easily done with a sharp pocket-knife or razor, if the

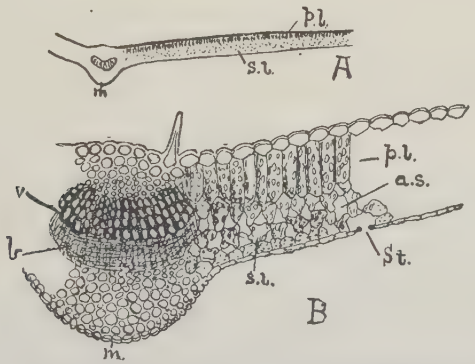


FIG. 68.—Structure of a cross-section of the leaf-blade of the Privet. A, As seen with a lens. B, More strongly magnified. *a.s.*, air-space; *o*, bast; *m*, midrib; *p.l.*, palisade layer; *s.l.*, spongy layer; *St.*, stomate (in cross-section); *v*, vessel.

leaf is rolled up), and examining the cut surface with a lens, the gross internal structure can be recognised (Fig. 68 A). Beneath the skin on the upper side of the leaf the tissue appears more compact and greener, and is seen to consist of elongated cells whose long axis is at right angles to the surface (*p.l.*); this is the so-called *palisade layer* which contains most of the chlorophyll. The lower part of the blade is of looser texture and lighter green and is consequently known as the *spongy layer* (*s.l.*). The stomates in the lower skin (Fig. 68 B, *St.*) open into the numerous air-spaces (*a.s.*) between the cells of the spongy layer; these spaces form a connected system throughout the

leaf and thus the carbon dioxide diffuses into the cells and comes into close contact with their chlorophyll. Since most of the latter is contained in the palisade layer, a feature to which the darker colour of the upper side of the blade is due, starch-formation is most active in this region. Near the centre of the cross-section lies the bulging midrib (*m*) in which the small vessels (*v*), serving to convey water and mineral salts to the leaf, can be recognised.

An experiment was described in the first chapter (p. 10) illustrating the importance of *chlorophyll* in carbon dioxide assimilation, a fact that can also be proved by applying the Iodine-test to variegated leaves (*e.g.* variegated Privet). If a rough sketch of the blade be made before it is decolourised, the starch-reaction will be found to appear only in those patches which were formerly green. In view of its importance in the assimilatory process, the properties of chlorophyll may next be studied more fully.

If a chlorophyll-solution is obtained in the way described on p. 10, it will be seen to have a deep green colour when held up to the light, but when held against a black background, so that the light is reflected from it, the solution appears a dark reddish-green. It will be a familiar fact that daylight is a combination of rays of all colours, and our previous observation shows that the red rays are absorbed (hence the reddish tinge in reflected light), whilst the others give the characteristic chlorophyll-colour when viewed in transmitted light. This may be verified by examining daylight, or other white light, that has passed through a chlorophyll-solution with the aid of a spectroscope (see Appendix XVII.), when a dark absorption-band will be readily recognised in the red zone; other absorption-bands (in the orange and yellow zones) are also present, but these are smaller and more difficult to see, whilst a large part of the blue and violet zones is generally obliterated.

It has already been mentioned above (p. 127) that in the absence of Iron-compounds chlorophyll is not formed, and a similar result was noticed in the case of plants grown in the dark [1] (p. 10). Addition of Iron-compounds on the one hand or exposure to light on the other, however, soon lead to the ap-

[1] Such an absence of chlorophyll through growth in the dark is exhibited by the leaf-stalks of cultivated Celery and Sea Kale.

pearance of the green colour. Apart from these two essentials for chlorophyll-formation, a suitable temperature is also necessary, the pale colour of the shoots of many plants that commence to grow early in spring being a result of imperfect production of the green matter. Finally, attention may be drawn to the fact that intense light tends to decompose chlorophyll; thus, if two test-tubes containing a solution of it are kept, the one in strong light, the other in darkness, the former will soon lose its fresh green colour (in contrast to the latter) and become a dirty brown.

The light absorbed by chlorophyll is doubtless effective in assisting in the formation of starch, although the exact part which it plays is still disputed. The necessity of light for starch-formation in the leaves of an entire plant was demonstrated by the experiment described on p. 10, and a modification

FIG. 69.—Starch-print. The leaf shown has been covered with a stencil-plate bearing the letter G, exposed for some hours to sunlight, then decolourised and placed in Iodine-solution.

of the same method is applicable to individual leaves. Thus, if half the leaf of a plant, which has been kept in darkness till it shows no starch-reaction, is covered over with silver paper, whilst the other half is left exposed, starch will be formed only in the illuminated part. Again, if a similar leaf is covered with a stencil-plate (Appendix XVIII.) and placed in the light, subsequent treatment with Iodine will give a dark letter on a light ground (cf. Fig. 69).

Starch, which so commonly constitutes the first easily recognisable product of carbon dioxide assimilation or photosynthesis, belongs to a group of complex substances known as *carbohydrates*; the name is due to the fact that these compounds contain the three elements Carbon, Hydrogen and Oxygen, the last two being present in the same relative proportions as in water (H_2O). Thus, the chemical formula of starch

is $n(C_6H_{10}O_5)$,[1] and the presence of Carbon can be demonstrated by strongly heating starch in a dry test-tube, when most of the Carbon remains behind as a black mass. There are many other kinds of carbohydrates that are found in the plant, for instance sugars, which would show similar changes on heating as in the case of starch.

It is known, however, that starch is not really the first substance formed in photosynthesis, but that others, such as sugars (*e.g.* grape sugar, $C_6H_{12}O_6$), intervene; in fact, in many Monocotyledonous plants the leaves rarely produce starch, sugars being the customary final product of carbon dioxide assimilation in such cases. But in most Dicotyledons these sugars undergo the further change into starch, and it is not difficult to show that such a conversion can take place. If detached starch-free leaves of the Canadian Pondweed are placed in a 5 per cent. solution of grape sugar in the dark, starch can subsequently be demonstrated in them in the usual way.

The chemical change involved in the production of carbohydrates like grape sugar from carbon dioxide and water can be indicated by the following equation :—

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2.$$

Carbon dioxide. Water. Grape sugar. Oxygen.

Chemists have not yet succeeded in carrying out this process,[2] which is probably due to their being unable to supply the requisite energy, such as the plant obtains from sunlight with the help of its chlorophyll. For, when a relatively complicated substance like a carbohydrate is built up from two such simple compounds as carbon dioxide and water a large quantity of energy is expended, which remains in the carbohydrates in a latent form, but becomes liberated when the latter break down. Since light furnishes the energy, we are now in a position to

[1] The *n* prefixed to this formula means that it is not known what multiple of $C_6H_{10}O_5$ correctly represents the molecule of starch.

[2] There is no doubt that such a relatively complicated body as grape sugar is not the first to be formed in photosynthesis, but it has not yet proved possible to ascertain certainly what substance or substances precede it; many botanists hold that formaldehyde (CH_2O) is the first product.

understand why it is so essential to the formation of the first products in assimilation.

The above equation shows that in the production of carbohydrates in the green leaf Oxygen is given off and that the volume of this latter is equal to that of the carbon dioxide taken in. The liberation of Oxygen can be demonstrated by the following experiment (Fig. 70): A bunch of Canadian Pondweed or other water-plant (land-plants being much less suitable

Fig. 70.—Apparatus to demonstrate that an assimilating water-plant gives off Oxygen. For description, see text.

for this purpose, cf. p. 332) is placed in a cylinder of water (*c*) with the cut ends beneath an inverted funnel *f*, which is completely submerged and suspended as shown in the figure. A test-tube (*t*) full of water is inverted over the stem of the funnel and the whole apparatus is placed in bright light. Bubbles are seen to rise from the cut ends into the test-tube and, displacing the water, collect at the top; in this way after some hours a considerable quantity of gas is obtained. When all the water in the test-tube has been driven out, the usual glowing splinter test

will show that the contained gas consists mainly of Oxygen. If at the same time a similar apparatus is fitted up, except that water which has been boiled (and subsequently cooled) is employed, no liberation of Oxygen will be observed, even in strong light. This is because in boiling all the carbon dioxide dissolved in the water was driven off, thus rendering assimilation impossible. The experiment also shows us that aquatic plants depend on the carbon dioxide dissolved in the water for their assimilatory process, a fact which is also apparent if we apply the Iodine-test to the leaves of such a plant grown in boiled water.

A modification of the experiment above described will enable us to investigate the influence of different light-intensities, different temperatures, and different amounts of carbon dioxide on the process of photosynthesis. For this purpose we use a single shoot of some water-plant, loosely tied to a long glass rod in such a way that the cut end points upwards, the whole being placed in a cylinder of water. In bright sunlight bubbles arise from the cut surface at a considerable rate, but their number is much diminished when the cylinder is placed in the shade and still more so in a poorly illuminated room, whilst in the dark there are practically none. We thus see that, other things being equal, the rate of assimilation (as measured, for instance, by the number of bubbles per minute) decreases with the intensity of the light. The same method shows that it also diminishes as the temperature of the water is lowered and almost ceases when several lumps of ice are added. A siphon of soda-water enables us to increase the amount of carbon dioxide present in solution, and we can thus prove that the greater the amount of this gas available the more rapid is the assimilatory process.

Our discussion of photosynthesis has shown how water from the soil and carbon dioxide from the air are converted, with the help of the chlorophyll under suitable light- and temperature-conditions, into carbohydrate food-substances whose further fate must now be considered. Part of the carbohydrates, together with nitrates, sulphates, and phosphates brought up in solution in the soil-water, are built up into still more complex substances containing, apart from Carbon, Hydrogen, and Oxygen, the elements Nitrogen, Sulphur, and frequently also

Phosphorus; these bodies are spoken of collectively as *proteids* and, as we have already seen (p. 127), the Calcium, Magnesium, and Potassium salts play some part in their formation. It is specially elaborate proteids that constitute the living proto plasm of plant-cells.

The carbohydrates which do not undergo these changes are in part modified to form the *cellulose*, of which the walls of the cells are largely composed, whilst the remainder are transferred from the leaf to other organs, where they are either used directly for growth or become stored up as a reserve. Carbohydrates are continually being thus conducted away from the seat of their formation, but on a bright day they are produced in photosynthesis more rapidly than they can be removed and consequently, towards the end of the day, the leaves exhibit an accumulation of starch which, however, disappears again overnight. This transference of carbohydrates can be readily demonstrated in any plant, whose leaves form plentiful starch, by comparing the amount of the latter in a leaf removed at sunset and in one picked early the following morning. On the other hand, detached leaves with their petioles in water do not lose their starch during the night, since it cannot be removed. Proteids which are probably in large part built up in the leaves, since it is here that the materials for their production are chiefly found, are conveyed away in a similar manner. In all cases the material thus transferred is mainly in solution.

A demonstration of the course followed by the elaborated food-substances in travelling from one part of the plant to another can be obtained in the following way: A ring-shaped piece (extending in as far as the wood) is cut from the bark of a fresh twig of a Willow (Fig. 71 B) below the uppermost node. The twig is now suspended in a tall wide cylinder containing a little water, the sides being lined with wet blotting-paper and, as a control, a similar twig which is not ringed is placed beside it. After some days the buds on the twigs will commence to sprout and adventitious roots to develop from below each node (cf. p. 57); all the axillary shoots, with the exception of the uppermost one, should now be removed from each twig, so that the adventitious roots arising from the lower nodes depend upon the leaves of the top shoot for food-material. At the end of about five weeks it will be found that the roots of the un-

ringed twig are much more vigorously developed than those below the point of ringing on the other twig (Fig. 71).

This shows that, by the removal of the tissues outside the wood, the passage of food-material to the lower portion is prevented. If the one twig is split open lengthwise above the point of ringing, treatment with Iodine will disclose considerable accumulations of starch above the spot at which the outer tissues have been interrupted, thus proving that the latter are

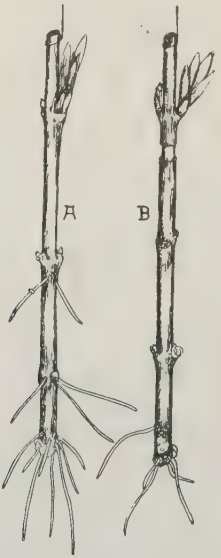


FIG. 71.—Twigs of the Willow; B, ringed; A, unringed (half the natural size). For further details, see text.

the regions through which the materials elaborated in the leaves are conducted to other parts of the plant.

As a matter of fact a delicate tissue known as the *bast* and invariably situated just outside the wood (Fig. 72 A, *b*) of the stem (cf. p. 112), is largely responsible for the transference of elaborated food-materials. This tissue is well seen in the Vegetable Marrow (Fig. 60 *b*), where, however, a second group of bast occurs on the inner side of each woody strand, an arrangement which is not very common amongst British plants. Similar groups of bast are situated on the under side of the woody

strands in petiole and leaf-blade (Fig. 68 B, *b*), but are difficult to detect without the help of a microscope. In the root they combine with the wood to form the central core and, in a cross-section of one of the larger roots of the Creeping Buttercup (Fig. 72 B), can just be discerned with a lens as lighter-coloured masses (*b*) alternating with those of the wood (*w*) which appear like a five-rayed star.[1] Thus the bast is present in all parts of the plant and indeed, like the wood, forms a continuous tissue, the two together constituting the so-called *vascular system*.

During the numerous chemical changes that lead up to the

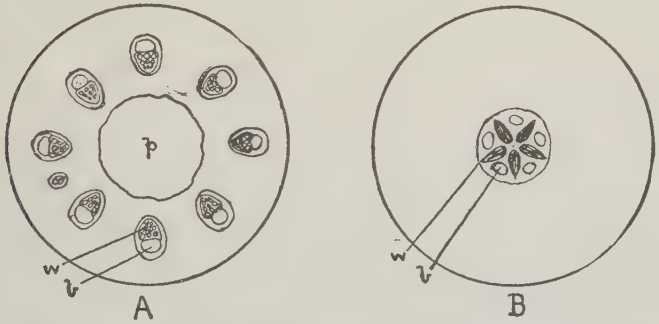


FIG. 72.—Cross-sections of A, the stem, and B, the root of the Creeping Buttercup (considerably magnified). *b*, bast; *p*, hollow pith of stem; *w*, wood. In the wood of the stem the vessels are recognisable.

formation of proteids and protoplasm a large number of other substances are formed, many of which are not further used in nutrition; analogous compounds, moreover, are produced in the breaking down processes which are constantly taking place in the plant (cf. Chapter XIV.). Examples are furnished by the bright colouring-matters of many petals the ethereal oils of many sweet-smelling herbs and flowers, and the vegetable acids found in such fruits as the Lemon. In many cases parts of the plant contain substances which are disagreeable to the taste or even poisonous; such are the tannins which are responsible for the astringent taste of Acorns, many young fruits (*e.g.*

[1] The wood throughout the plant can be readily distinguished from the adjacent bast by the fact that it stains deep yellow with Iodine.

Pears), and young Bracken-leaves, whilst alkaloids and similar substances are the cause of the poisonous properties of the Monkshood, Foxglove, Deadly Nightshade and many Toadstools. The presence of such substances generally renders the plant more or less immune from browsing animals.

The resin which is often seen exuding in quantity from wounded stems of Conifers is another of these bye-products and probably is of importance in covering up injured parts with an antiseptic layer. In many plants (*e.g.* the Garden Poppy, Spurge, and Dandelion) a white or coloured milky juice, the *latex*, issues from any cut surface; this, though no doubt partly nutritive in function (since it generally contains proteids), rapidly congeals on exposure to the air and thus, like the resin, covers up a wound. The latex generally contains a small quantity of caoutchouc-particles, but in some tropical plants these are so numerous as to form the source of the rubber of commerce.

During proteid-elaboration crystals of calcium oxalate are generally produced in considerable amount, and in some cases these take the form of small bundles of minute needles, easily seen with a lens in the Ivy-leaved Duckweed and in the leaves of the Enchanter's Nightshade as short dark lines irregularly scattered through the tissues. In old stalks of Rhubarb the gritty taste is due to the abundant crystals of calcium oxalate. Where these crystals occur in large quantities they probably render the plant unpalatable to Snails and other small animals.

CHAPTER XI

Special Methods of Nutrition

In contrast to animals, the ordinary green plant builds up its body from simple chemical compounds obtained directly from the soil and air, and thus plants are the great constructive force in nature. The animal depends entirely on elaborated food-substances (*e.g.* carbohydrates, fats, proteids) and therefore obtains its nutriment second-hand, either directly from the Vegetable Kingdom or indirectly (in the case of Carnivores) from other herbivorous animals ; so that, if green plants were to disappear from the surface of the earth, almost the whole living universe would shortly perish.

There are plants, however, which are more or less dependent on elaborated food-substances and can only thrive when the latter are available in the form of, either living or dead, organic matter. In such plants the leaves are always of small size and frequently devoid of chlorophyll. When part or all of the food is obtained from some other living organism the plant is known as a *parasite* and the organism on which it feeds as the *host,* whilst when the source of nourishment is dead organic matter we speak of a *saprophyte.*

As a first example of the former class we may consider those plants which are only partly dependent on their host and are consequently described as *semi-parasites.* These still retain the power of producing a considerable amount of chlorophyll and their leaves, though relatively small, are green and often larger than those of a true parasite. As a result, these plants can grow independently of a host, although under these circumstances they are far less vigorous. Good examples are furnished by the Red Eye-bright (*Bartsia,* Fig. 73 A), the Cow-wheat, the Eye-bright, and the Yellow Rattle, all of which

generally grow in meadows and are parasitic on the roots of the surrounding vegetation, particularly Grasses. If one of these plants is carefully dug up with a good deal of the accompanying

FIG. 73.—A, Overground portion of a plant of the Red Eye-bright with numerous flowers (natural size). B, Root-system of the same, showing connection with roots of host (somewhat enlarged). C, A small part of the last (much enlarged). *h*, root of host; *S*, sucker.

soil and the latter gently washed away with water, the roots of the parasite will be found attached at certain points to those of the host (Fig. 73 B and C) by minute disc-like suckers (*S*) appearing as slight swellings. These penetrate into the roots of the

host as far as the central vascular core and thus absorb nourishment.

Among British flowering plants there are but few complete parasites, none of which are really common; they include the Dodder, the Toothwort (see Frontispiece), and the Broomrapes. As a typical instance we may select the Dodder which is an annual parasitic on many different hosts (*e.g.* Clover, Furze, Heather, etc.). The thread-like stem of this plant entwines the host (Fig. 75), some of the coils being close together and bearing the suckers (*S*) through which nourishment is absorbed,

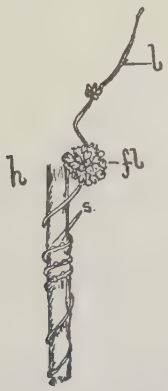


Fig. 75.—Small part of a plant of the Dodder, showing the method of entwining the stem of the host (slightly enlarged). *fl.*, flowers; *h*, stem of host; *l*, leaf; *S*, suckers.

whilst others are more distant and unattached. At first sight there appear to be no leaves, but careful examination discloses a number of minute scales (*l*) separated by long internodes and, as in all true parasites, completely devoid of chlorophyll. The stems vary in colour between bright yellow and red, and thus the plant becomes conspicuous, even before the rosette-like bunches of pink flowers (Frontispiece and Fig. 75, *fl.*) are formed. The Dodder agrees with all parasites in its extensive production of seeds, so that from a single parent-plant a large quantity of offspring will arise. In this way the risk of a host not being found is minimised, since one or other of the numerous seeds is very likely to germinate near a suitable plant.

The seedling of the Dodder does not show so marked a distinction into radicle, plumule and cotyledons as in the case of non-parasites, *i.e.* the extreme reduction of the vegetative parts seen in the mature plant appears already in the seedling. The latter is, however, capable of a brief independent existence, and during this period the tip of the stem swings round in a circular manner and may thus happen to meet with a support; thereupon the root withers, so that the mature Dodder has no connection with the soil whatever. Failing the presence of a host the seedling soon dies away.

The Dodder is exceptional among British parasites, not only in being a climber and in having no roots in the mature condition, but also in being attached to the stem of its host. Nearly all other British plants of this kind are so-called *root-parasites*—that is to say, like the semi-parasites already considered, they fix themselves by means of suckers to the roots of the attacked plant. This is the case in the Toothwort and the Broomrapes. The yellowish-white shoots of the former (Frontispiece) appear above ground in the early spring, flower about April, and are usually found beneath the Hazel or the Elm. The overground part consists of practically nothing else but an inflorescence of numerous purplish flowers, with membranous leaves intermingled. At a varying depth beneath the surface of the soil one meets with a perennial and extensively branched horizontal stem, the upturned tips of which constitute the annual aerial shoots. The whole underground system bears numerous decussate fleshy scales of a pink colour and richly branched adventitious roots which attach themselves to those of the host (Hazel or Elm) by flat suckers.

Owing to the absence of the usual transpiring surface, an excess of water readily collects within the parasite and in the Toothwort is exuded from water-glands lining the inner surface of the hollow fleshy scales borne on the underground stem. The foliage-leaves of the semi-parasites described above bear similar water-exuding organs, for in all these cases, apart from its own absorption, the parasite may at times receive more water from its host than it can cope with by transpiration.

The species of Broomrape, the commonest of which is found on the roots of Clover, are close allies of the Toothwort and very similar in their overground organs, except that they are usually

more or less brownish in colour. The seeds of these forms are stated to germinate only when in contact with the roots of a suitable host. In common with all the other parasites we have noticed, the Broomrapes exhibit a much reduced leaf-surface and very extensive seed-production, but even so they are by no means frequent. The characteristics just enumerated are, in our flora, best seen in the Dodder, but the reduction of the vegetative as compared with the seed-producing part has gone much further in the case of some tropical parasites, in which the vegetative organs are represented by one much-branched sucker traversing the tissues of the host.

The Mistletoe is a somewhat exceptional type of parasite found growing on the branches of Apple, Hawthorn, etc. It possesses green leaves, in this respect resembling the semi-parasites, and sends its peg-like suckers (whose growth in length keeps pace with the increase in thickness of the branch) deep down into the wood of the host. It differs from most other British plants, not only in its parasitic qualities, but also in growing aloft on the branches of trees. This kind of situation is, however, frequented by many non-parasitic plants of the Tropics (*e.g.* Orchids), as well as by the common Polypody of our own country (Plate III., Fig. 181).

The commonest saprophyte amongst British flowering plants is the Bird's-nest Orchid; other examples, all of them rare, are the Bird's-nest (a member of the Heather-family) and the Coral-root Orchid. All these forms are found in shady situations growing among the humus, the Bird's-nest Orchid being especially characteristic of dense Beech-woods. This saprophyte (Fig. 77) blooms in late May, the plant emerging from the humus as an unbranched stem bearing a few scaly leaves (*l*) of moderate size and numerous flowers (*fl*), all of a brown colour, little or no chlorophyll being present. The erect shoots are borne on a subterranean portion (*n*), the numerous branches of which are interwoven so as to form a structure somewhat resembling a bird's nest; hence the common name. Such a saprophyte obtains its nourishment from the organic matter in the humus and can consequently only thrive in places where there is a plentiful accumulation of the latter.

Although parasites and saprophytes are rare amongst flowering plants, a large number of simpler forms of plant-

life lack chlorophyll and adopt these methods of nutrition. It is a familiar fact that organic substances (*e.g.* bread, jam,

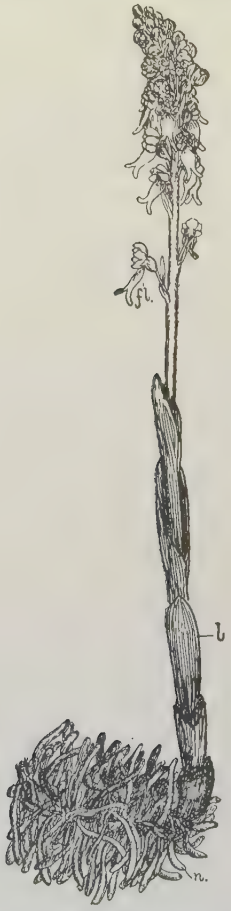


FIG. 77.—Complete plant of the Bird's-nest Orchid (about two-thirds natural size). *fl.*, flower; *l*, leaf; *n*, the underground nest-like portion.

fruit) in a state of decay soon become mouldy, and these Moulds with their richly branched thread-like body (Fig. 78) are saprophytic plants obtaining their nourishment from the decaying

matter. Similarly, Mushrooms, Toadstools, Puffballs (Fig. 79), and many other Fungi live saprophytically on the abundant humus of woodlands, where they frequently abound in the

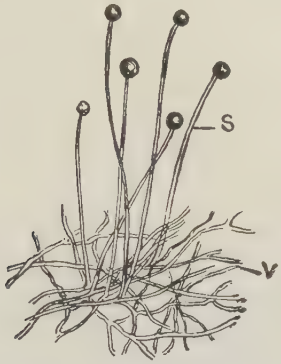


FIG. 78.—A small part of the Common Mould of bread (considerably enlarged). *v*, the creeping vegetative portion; *s*, the upright reproductive branches.

FIG. 79.—Photograph of a group of seven Puffballs and one Toadstool. [Photo. E. J. S.]

autumn. In these forms the overground portion consists usually of the reproductive body alone, whilst the actual vegetative part resembles that of the Moulds and is hidden beneath the soil.

Many of the Fungi, however, are parasites and cause some

of the most pernicious diseases of cultivated plants, as well as occasionally of animals. Examples are afforded by the Rust of Wheat, the Smut of Oats, the Gooseberry Mildew, and the Salmon-disease. The Bacteria, moreover, are parasitic or saprophytic plants of a simple type (many consisting of but a single cell), the former being responsible for many virulent diseases (*e.g.* cholera, typhoid, etc.), whilst the latter are often highly beneficial in furthering processes of decay in nature.

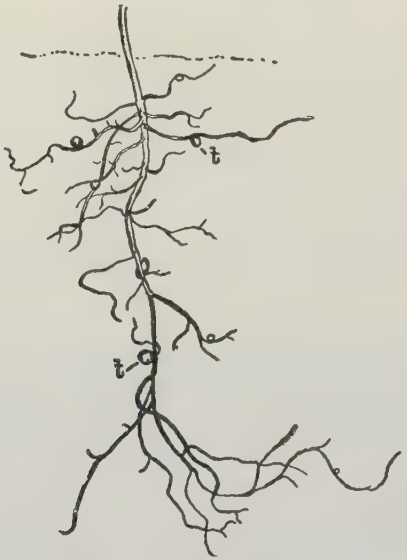


FIG. 80.—Root-system of the Meadow Vetchling (*Lathyrus aphaca*), showing the root-tubercles (*t*) (natural size). The level of the soil is indicated by a dotted line.

All higher saprophytes are unable to utilise the humus directly, but require the aid of Fungi which live in the soil and frequent the outer tissues of the underground organs of the saprophyte. Such an association with Fungi is, however, not confined to plants of this type, but is seen in many other forms (*e.g.* the Conifers, the Beech, and most members of the Heather-family), all of which grow where humus is plentiful. In many cases the threads of the Fungus form a complete investment to the young parts of the root-system and thus, not only take over

the water-absorbing functions of the root-hairs (which are absent in such plants), but also no doubt aid in the taking up of organic matter from the humus.

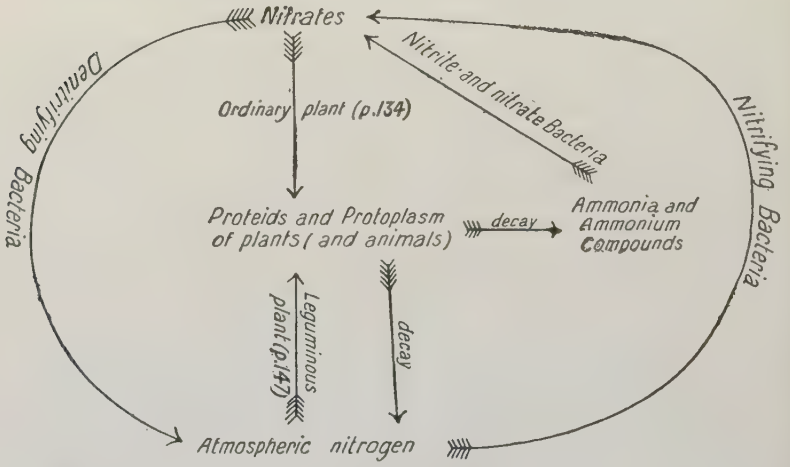
A similar association between roots and Bacteria is met with in most members of the Pea-family (Leguminosæ). On digging up a plant of the Bird's-foot Trefoil or a Vetch we shall find that the roots bear a number of small swellings (Fig. 80, *t*, Meadow Vetchling), the so-called *root-tubercles* in which the Bacteria occur. If two plants of this family are grown from seed, one in ordinary soil, the other in soil which has been thoroughly baked so as to kill all the contained life, the former will be seen to grow vigorously and develops plenty of tubercles on its roots, whilst the latter is not so robust and has roots without tubercles. This shows not only that soil-Bacteria are responsible for the formation of the swellings, but also that their presence is necessary to the proper nourishment of the plant.

As a matter of fact, among the countless Bacteria which inhabit the soil there are some which, unlike most vegetable organisms (p. 127), are able to use the Nitrogen of the air and convert it into compounds available to the ordinary plant. A certain group of these Bacteria invade the root-hairs of members of the Pea-family and in this way cause the swellings to form. Within the tubercles the Bacteria multiply rapidly by a process of division and ultimately a considerable number of them are digested by the plant, whilst the remainder return to the soil when the roots decay. As a result of their association with these Bacteria, the Leguminosæ not only obtain the ordinary supply of Nitrogen (in the form of dissolved nitrates and ammonium-compounds), but also receive Nitrogen indirectly from the air. It is for this reason that a growth of Clover or Lucerne is useful in replenishing the available Nitrogen-compounds in the soil, after these have been diminished by previous crops of Cereals. Such a rotation is quite customarily resorted to by farmers, the Leguminous crop at the end of the season being allowed either to decay or being ploughed into the soil as " green manure."

Both in the case of these Bacteria and in the fungal threads inhabiting the roots of higher plants it is probable that the invading organism itself derives some benefit from the association, perhaps by receiving from its host elaborated food-

materials which are necessary to its existence and are not found in the surrounding soil.

Apart from those just considered there are other soil-Bacteria which live independently and convert free Nitrogen into available compounds (*nitrifying Bacteria*). Still others oxidise ammonium-compounds, which are always formed in the decay of plants and animals, to nitrites and ultimately to nitrates. It may be added, however, that certain soil-Bacteria carry on a reverse process—that is to say, they break up nitrogenous compounds with evolution of free Nitrogen which escapes into the atmosphere (*denitrifying Bacteria*). In view of the absolute necessity of Nitrogen-compounds (especially nitrates) to the ordinary plant, these different processes are of supreme importance and may be briefly epitomised as follows :—



There is thus a continual circulation of Nitrogen in nature, and the different organisms concerned evidently work sufficiently well in unison to maintain the balance.

The presence of Bacteria in the soil can be demonstrated in the following way: Three clean saucers, sterilised by placing them in boiling water, are filled with a solution of gelatine (10 parts of gelatine to 100 of water). We then take a little garden earth and divide it into two parts, one of which is thoroughly baked; thereupon each lot of soil is shaken up with boiled

water which has cooled, and a few drops from each liquid is added to distinct saucers of the gelatine just before setting. The third saucer is left untreated as a control, all three being covered with sterilised glass plates. After some days the gelatine to which water from the unbaked soil was added will show a number of white patches (due to Bacteria), whilst few or none are to be seen in the other two saucers.

There is still one other special method of nutrition that remains to be considered, viz. that of the so-called *insectivorous plants*. A common example is the Sundew (Fig. 81) which frequents boggy situations, such as damp moorlands

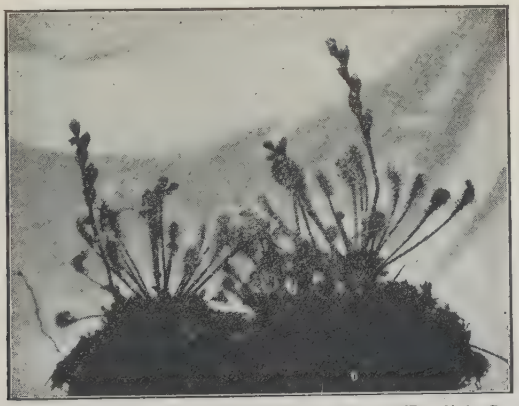


FIG. 81.—Photograph of two plants of the Great English Sundew. On one of the leaves of the left-hand plant an insect (*ins.*) has been caught. *bl.*, leaf-blade ; *infl.*, inflorescence ; *p*, petiole. [Photo. E. J. S.]

and peaty heaths. The plant consists of a radical rosette of reddish leaves which are provided with relatively long petioles (*p*), expanding into a blade (*bl.*) which is rounded or oval according to the species ; from the centre of the rosette arise one or more upright inflorescences (*infl.*) with white flowers. The upper surfaces and the edges of all the leaf-blades are beset with numerous hair-like outgrowths or tentacles having swollen ends which glisten owing to a sticky covering (see Fig. 81). Insects attracted by the latter alight on the leaf and adhere to the secretion upon the ends of the tentacles. If the insect be powerful enough, it may in its struggles manage to escape, but unless

this happens at once the tentacles bearing the insect begin to bend slowly towards the middle of the blade, and this is soon followed by a similar movement of the others.

In this way the insect's body is firmly held against the surface of the leaf, in fact it is often completely hidden from view by the incurved tentacles. At this stage digestive juices pass out from these structures and, attacking the insect's body, slowly convert its soft parts into a soluble form suitable for absorption by the plant. After a considerable lapse of time the tentacles

FIG. 82.—Photograph taken from above, showing the leaf-rosettes of a considerable number of plants of the Butterwort. At the top left-hand corner is a specimen of the Cross-leaved Heath and on the right, near the top, the trailing shoots of the Bog Pimpernel. [Photo. E. J. S.]

resume their normal position and now the undigested hard portions of the insect alone remain. The Sundew is able to live without such insect-food, but under these circumstances it produces fewer flowers and seeds—in other words, its vigour is much diminished.

The Butterwort (Fig. 82) captures its prey in a somewhat similar manner. Here the upper surfaces of the yellowish radical leaves bear numerous sticky glands, some of which serve to entrap the insect, whilst others digest its body. A

peculiar case is afforded by the Bladderwort, a submerged water-plant bearing numerous little sack-like structures on its deeply divided leaves (Fig. 83 A, *bl.*). Each of these bladders has a narrow aperture (Fig. 83 A, *o*) surrounded by hairs and closed by a trap-door opening only inwards (Fig. 83 B, *t*); hence minute water-insects pushing their way into the trap remain imprisoned and ultimately die, when the products of their decay are absorbed by the plant.

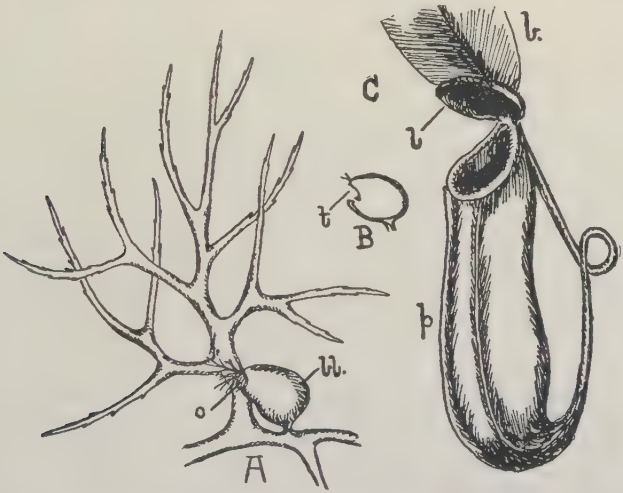


FIG. 83.—A, Single leaf of the Bladderwort (about three times the natural size). B, Single bladder of the same cut through lengthwise (same scale as in A). *bl.*, bladder; *o*, aperture of bladder; *t*, lid of bladder. C, Single pitcher of the Pitcher-plant (*Nepenthes*) (somewhat reduced). *b*, leaf-like broadening of base of petiole; *l*, lid; *p*, pitcher.

Mention should also be made of the well-known Pitcher-plant, in which the blade is modified to form the pitcher (Fig. 83 C, *p*), whilst a broadening (*b*) of the lower part of the petiole fulfils the usual functions of the lamina; the rigid lid (*l*) serves to protect the contents of the pitcher from being flooded by rain. Insects which venture on to the slippery inner surface of the pitcher fall into the liquid, which occupies the lower part, and are prevented from crawling out by the numerous downwardly directed scales upon the wall; subsequently their bodies undergo digestion and the products are absorbed by the plant.

Most insectivorous plants frequent swampy localities, and it is probable that by their special method of nutrition they make up for some deficiency of necessary mineral salts in the water which they absorb.

Our study of the nutritive processes in plants has shown us that green leaves are the world's great factories, which build up complex from simple substances and store up the energy of the sunlight in a form available for the maintenance of their activities. More food is often elaborated in this way than is necessary for the plant's immediate requirements and the surplus is stored up for a two-fold purpose. For, as we have seen, such food-reserves not only further new growth by supplying materials to sprouting buds in the spring, but also enable the parent-plant to provide the necessary start in life for its offspring, whether these arise from seeds or from organs of vegetative propagation.

CHAPTER XII

Food-Storage and Vegetative Reproduction

In discussing creeping plants we noticed that one of the great advantages of this habit lies in the rapidity with which a considerable surface of the ground is covered (cf. p. 19). Tufts of adventitious roots are produced from some of the nodes of the prostrate shoots (*e.g.* in the Creeping Jenny and Ground Ivy, Fig. 8) and thus, if the older parts die away, the rooted branches become free as independent plants. A similar propagation by horizontal creeping shoots, which arise from the

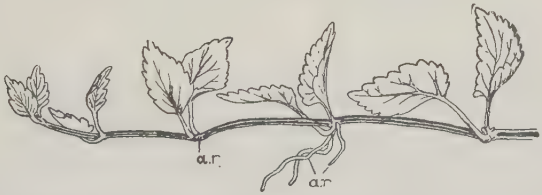


Fig. 84.—Creeping shoot of the Yellow Dead-nettle (about half natural size). The upright flowering axis from which this shoot arises is not shown. *a.r.*, adventitious roots, fully developed at one node, as rudiments at another.

base of the erect flowering stem and subsequently lose their connection with the main plant, is seen in the Yellow Dead-nettle or Archangel (Fig. 84) and the Bugle.

In many plants such creeping shoots are modified to form *runners* which are specially fitted for vegetative reproduction (*i.e.* propagation by detachment of some part of the vegetative organs) and are seen, for instance, in the Cinquefoil and the Strawberry (Fig. 85); as an example the latter may be described. Towards the end of the flowering season numerous slender branches arise from the axils of the radical leaves and radiate

in all directions over the surface of the ground. These runners elongate with great rapidity, forming long internodes and a few small scale-like leaves (*s.l.*); new plants are ultimately produced from the upturned tips of the runner, whilst the latter is continued by an axillary branch arising from a leaf of the new rosette, giving a sympodial construction. Adventitious roots (*a.r.*) arise from the base of the new plant and sooner or later the portion of the runner connecting it with the parent decays away. The distinctive features of the runner lie in its bearing only scale-leaves and in its considerable elongation,

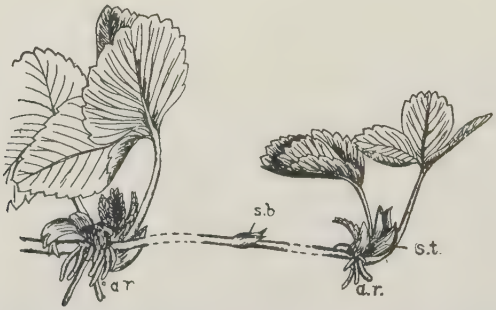


FIG. 85.—Runner of the Strawberry (about half the natural size). One plant produced from a runner is seen on the left, a younger one on the right. The runner is by no means indicated at its full length, being about four times as long. *a.r.*, adventitious roots; *s.l.*, scale-leaf; *st.*, stipule.

which serves to remove the daughter-plants from competition with the parent.

A special case of vegetative reproduction on the part of overground shoots is seen in the Bramble (Fig. 86), in which some of the woody stems arch over towards the ground and, on reaching the latter, exhibit a swelling of their tips from which numerous adventitious roots arise. From the axils of small leaves, which occur intermingled among the roots on the overground part, leafy shoots develop and produce a new Bramble-bush which after a time becomes independent. Thus the Bramble multiplies by rooting branches comparable to cuttings (p. 57).

The *suckers* found in many fruit-trees (*e.g.* Damson, Apple), as well as in the Poplar and the Yarrow (Fig. 87), are axillary

underground shoots which almost immediately turn up and come above the surface, when their tips give rise to new plants that remain connected with the parent for some time. As a

Fig. 86.—Rooting branch of the Bramble with numerous adventitious roots arising from the tip and showing one of the small leaves from which axillary shoots are produced (about two-thirds natural size).

consequence of this prolonged attachment the daughter-plant is nourished by the parent until it becomes fully established ; hence suckers are not swollen out with food-reserves like other

organs of vegetative propagation, to be subsequently considered, in which separation from the parent takes place before the daughter-plant is self-supporting. The underground portion of the sucker is of a white colour, but is readily distinguished from a root by the scale-leaves (*s.l.*) borne upon it. A consultation of Fig. 87 will show that here again we have a sympodial construction, the main axis for any season being a lateral branch of that of the previous season.

In many plants a portion of the stem is situated beneath

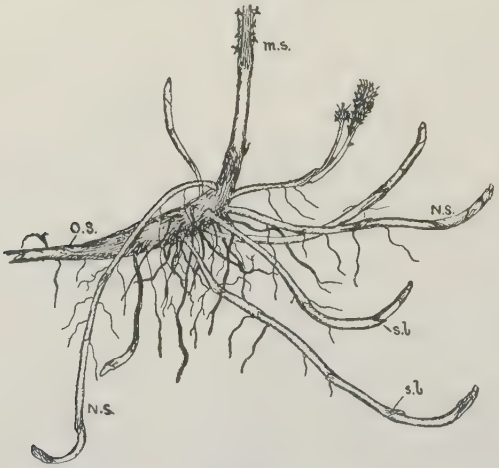


FIG. 87.—Base of a plant of the Yarrow or Milfoil, showing the remains of an old sucker (*o.s.*), whose upturned tip produced the main stem (*m.s.*), and numerous new suckers (*n.s.*) (about two-thirds natural size). *s.l.*, scale-leaves.

the surface of the soil, such underground stems when they creep horizontally being termed *rhizomes*, whilst the short more or less erect structures seen in the Buttercup, Primrose, and Wood Sanicle are known as *root-stocks*. The Solomon's Seal furnishes us with an instance of the former type. Here the aerial flowering shoots will be found to arise vertically from a thick white rhizome (Fig. 88), situated at some depth in the soil and covered with ring-like remnants of scale-leaves (*s*), as well as with adventitious roots (*a.r.*) which occur principally upon the under side. Examination of an entire plant in spring

shows that the ends of the main axis of the rhizome and its branches curve up to form the overground shoots (*a.s.*), whilst a bud, from the axil of the lowest scale-leaf on the latter, continues the horizontal growth of each branch of the subterranean system; the latter, in the Solomon's Seal, is therefore sympodially branched.

Some time after flowering the aerial shoots die away leaving on the upper surface of the rhizome a large round scar (*sc.*), the so-called "seal," marked by numerous dots which represent the broken ends of the vascular strands. In the autumn (the stage shown in the figure) the buds developed from the base

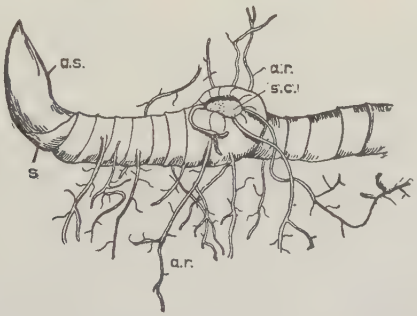


FIG. 88.—Rhizome of the Solomon's Seal in autumn (about half the natural size). *a.r.*, adventitious roots; *a.s.*, bud of next year's aerial shoot; *s*, scale-leaves on rhizome; *sc*, scar of aerial shoot of past season. The portion of the rhizome to the right of this scar was formed a year earlier than the part to the left of it.

of the aerial shoots have completed their horizontal growth, and their tips will now be found to have curved upwards, ready to grow above the surface of the soil in the following season. The rhizome persists for some time, so that several seals marking the annual flowering shoots may be found along its length, but sooner or later the older parts decay and as a consequence the branches become separate plants. Owing to large quantities of food-reserves stored up in the thick underground portion, the aerial shoots are able to grow rapidly in the spring and the detached daughter-rhizomes are well equipped for an independent existence.

The rhizome of the Solomon's Seal therefore serves not only

as an organ of vegetative propagation, but also for food-storage, and thus constitutes the means of persistence for this perennial from year to year (cf. p. 15). Similar examples are furnished by the Iris, the Lily of the Valley, the Sedges, and many Grasses. In all these cases the buds, as they grow forwards through the

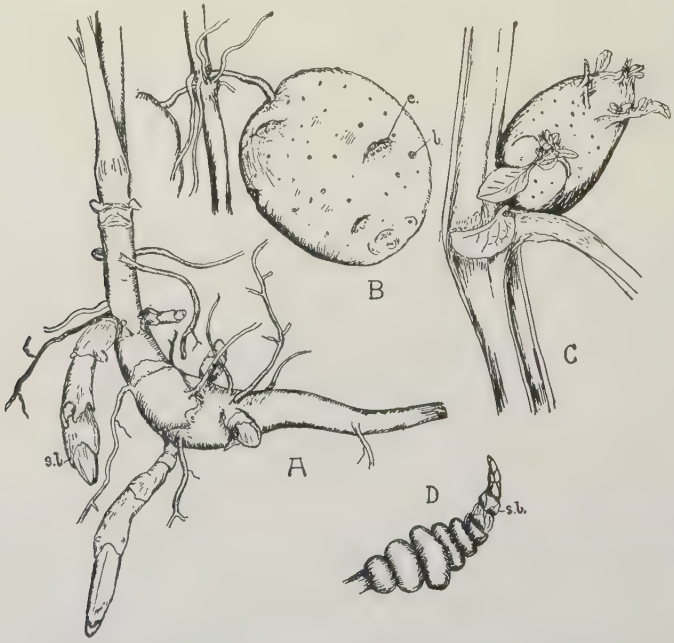


FIG. 89.—Food-storage in tuberous stems (all figures about two-thirds natural size). A, Perennial Sunflower. B, Potato (normal). C, Potato-tuber formed in axil of leaf of aerial shoot. D, Chinese Artichoke (tuber alone shown). *e*, "eyes"; *l*, lenticels; *s.l.*, scale-leaves.

soil, are encased in scales whose tips form a hard or even horny (*e.g.* Sand Sedge) point, well suited to pierce the ground.

Vegetative reproduction is likewise combined with food-storage in the Perennial Sunflower (Fig. 89 A), the Jerusalem Artichoke, and the Chinese Artichoke (Fig. 89 D), in all of which a number of axillary branches arise from scale-leaves on the underground part of the stem, in the course of the summer, and grow more or less horizontally through the soil. These shoots

bear scale-leaves (*s.l.*) showing the same decussate arrangement as the foliage-leaves. The food formed by the aerial shoot is in part stored up in the more or less swollen tips of the subterranean branches and, after the plant has died down in the autumn, the latter become detached, giving rise to new and independent plants in the following spring; each of these thus really represents a lateral branch of the plant of the previous season. In the case of the Chinese Artichoke (Fig. 89 D) the swollen tips exhibit a succession of swellings, each representing an internode, whilst in the Jerusalem Artichoke they form large tuberous structures of irregular shape. The large quantity of food-materials stored up in these organs renders them valuable as vegetables.

The *tubers* of the Potato are formed in the same way, but differ from the cases previously considered in having a thick corky protective covering (the peel), pierced by lenticels (Fig. 89 B, *l*) for purposes of gaseous exchange. The "eyes" (*e*), which are best seen on young tubers, represent the scale-leaves with their axillary buds; in practice, the Potato is cut up into pieces, each including an "eye," which thus serve as the starting-points for as many new plants. Under exceptionally favourable conditions some of the axillary buds on the overground parts of the plant occasionally develop into similar tubers (Fig. 89 C) and here the true character of the scale-leaf and axillary bud is very obvious.

The *corm* of the Crocus is a special kind of tuber formed by a swelling up of the base of the flowering stem, as can be seen if one examines a plant in April. If we halve the lower part of the specimen lengthwise, as in Fig. 90 D, we shall see the new corm (*c. 1914*) arising as a swollen structure enclosed within the sheathing bases of the lower leaves of the flowering shoot (*a.s.*), whilst below it is the corm (*c. 1913*) from which the latter has arisen. Later in the season, when the flowering shoot has withered, the new corm will be found to have increased greatly in size, the old one having shrivelled considerably, so that it is now the smaller of the two. In the autumn the corm has attained its full dimensions, is enveloped in the brown tunic (*i.e.* the remains of the sheathing leaf-bases mentioned above), and has produced one or more buds (Fig. 90 B, *b*) in the axils of the dead leaves of last spring's shoot; beneath it is a

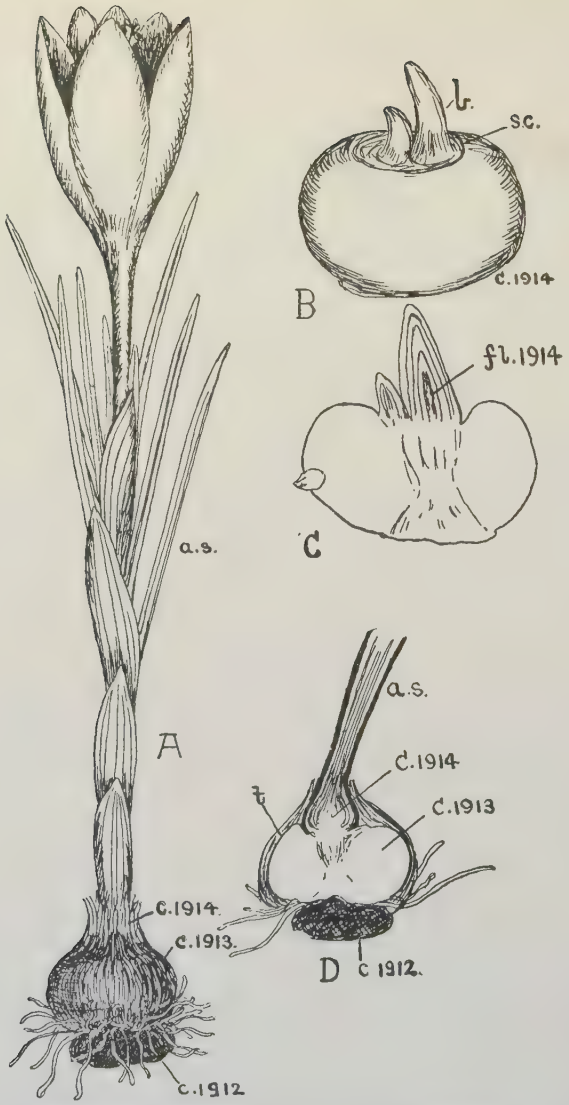


FIG. 90.—Development and structure of the Crocus-corm. **A**, Spring-condition with overground flowering shoot. B, Winter-condition of corm, showing two buds which will produce flowering shoots in the subsequent season ; one of the scales has been removed near the top of the corm, leaving a ring-shaped scar (*sc.*). C, Longitudinal section of the corm at the stage shown in B ; all scales removed. D, Longitudinal section of base of corm and flowering shoot at stage shown in A. (All figures about natural size.) *a.s.*, aerial flowering shoot; *b*, buds for next season's flowering shoots; *c. 1912*, *c. 1913*, *c. 1914*, corms of successive years ; *fl. 1914*, flower which will unfold in 1914 ; *t*, tunic.

dark mass, the remnant of the old corm (cf. Fig. 90 A and D, *c. 1912*).

The corm is thus a much swollen stem-base ensheathed in scales and bearing one or more axillary buds, in each of which the young leaves and flower for next year's growth (Fig. 90 C) can be recognised. On removing the scales it will be found that each of them is attached around the whole circumference of the corm (Fig. 90 B, *sc.*), whilst at the top of the latter the scars left by the withered flowering stem and foliage leaves can be distinguished. In the following season the buds grow out to form

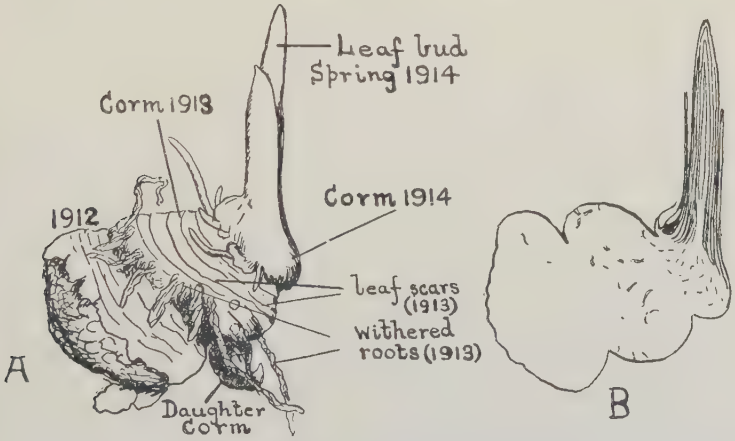


FIG. 91.—Corm of the Cuckoo-pint (*Arum*) in autumn (natural size). A, Entire. B, In longitudinal section.

the overground shoots and at the base of each of these the same sequence is repeated (Fig. 90 A and D). It will be realised that the corms of any given year are lateral to those of the previous year, so that the branching of the Crocus-plant is sympodial, each new segment being terminated by a flower. Inasmuch as the corms usually bear several buds and each of these gives rise subsequently to a separate daughter-corm, extensive vegetative reproduction is carried on.

The underground structure in the Cuckoo-pint is very similar, except that here the corms of previous years do not die away so rapidly (Fig. 91). In the autumn we find a well-developed leaf-bud for next year's growth, the base of which is already

prominently swollen to initiate the corm which will be completed in the subsequent season (corm 1914 in Fig. 91 A), whilst behind it are one or more corms of previous years (corm 1913, 1912) on which the ring-like leaf-scars and remains of roots are a prominent feature. The analogy to a fleshy rhizome, such as that of the Solomon's Seal, is very clear in this case, the construction again being sympodial. Other examples of corms are furnished by the Bulbous Buttercup and the Meadow Saffron.

The *bulb* of the Tulip (Fig. 92), Onion, or Hyacinth consists of a number of fleshy scale-leaves (Fig. 92 A, *fl.sc.*) encircling one another and the central bud (*f.a.*), the whole arising from a flat disc-like stem (*st.*) and surrounded by a thin brown papery investment (*i*) composed of one or more scaly leaves. If we halve a Tulip-bulb lengthwise, we can recognise in the central bud the parts of the future flower and a number of young foliage-leaves, whilst just within the flattened base are seen the rudiments of numerous adventitious roots (*a.r.*) appearing as small lines at right angles to the surface. In the axils of one or more of the fleshy scales will be found minute buds (*d.b.*), which will give rise to the new bulbs for the following season's growth. When the bulb begins to sprout, the adventitious roots exhibit a rapid growth (Fig. 92 B, *a.r.*) and, after they have become well established in the soil, the central bud elongates carrying up the foliage-leaves and the terminal flower which soon expands. This growth takes place at the expense of the food-substances stored up in the bulb-scales which consequently commence to shrink (cf. Fig. 92 B).

After flowering, the green foliage-leaves, as in the Crocus and Cuckoo-pint, persist for a considerable time ; during this period the food formed by them is passed down into the axillary buds of the bulb, which now exhibit a rapid increase in size (Fig. 92 B, *d.b.*). The latter also receive any food-material from the main bulb that has not been used up. When the overground shoot withers, we consequently find that the original bulb has been replaced by one or more daughter-bulbs which have developed from the axillary buds and are enclosed in the shrivelled papery remnants of the parent-bulb. The main axis of the latter is thus terminated by a flower (or, in the case of the Hyacinth, an inflorescence), the new bulbs being lateral branches from its base. When there are several daughter-

bulbs, the supply of food is sometimes not sufficient for an adequate development of all, and some of them consequently appear as small structures adhering to the surface of the larger

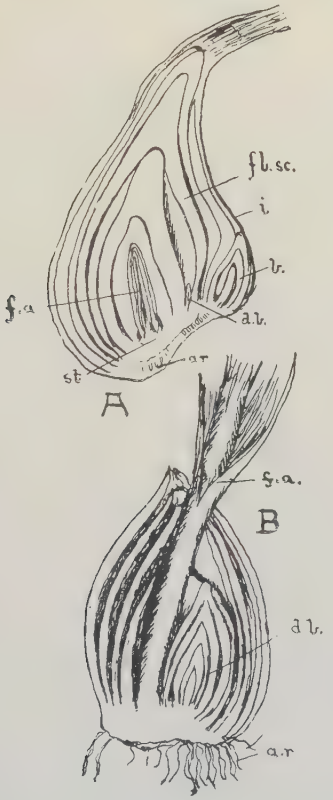


FIG. 92.—Structure and development of bulb of Tulip (natural size). A, Winter-condition in longitudinal section. B, Spring-condition in longitudinal section, only the base of the flowering axis being shown. *a.r.*, adventitious roots; *b*, incompletely developed daughter-bulb; *d.b.*, bud which will give rise to a daughter-bulb; *f.a.*, flowering axis; *fl.sc.*, fleshy scales of bulb; *i*, investment of dry scales; *st.*, flattened stem.

ones (Fig. 92 A, *b*). It will be realised that bulbs like those just described are really nothing more than huge buds in which most of the bud-scales are swollen with stores of food-material.

The bulbs of Narcissus (Fig. 93) or Snowdrop are, however, somewhat different. The fleshy scales of the bulb (Fig. 93 A, *l.f.s.*) here consist mainly of the swollen bases of foliage-leaves of preceding seasons (of the last year only in the case of the Snow-

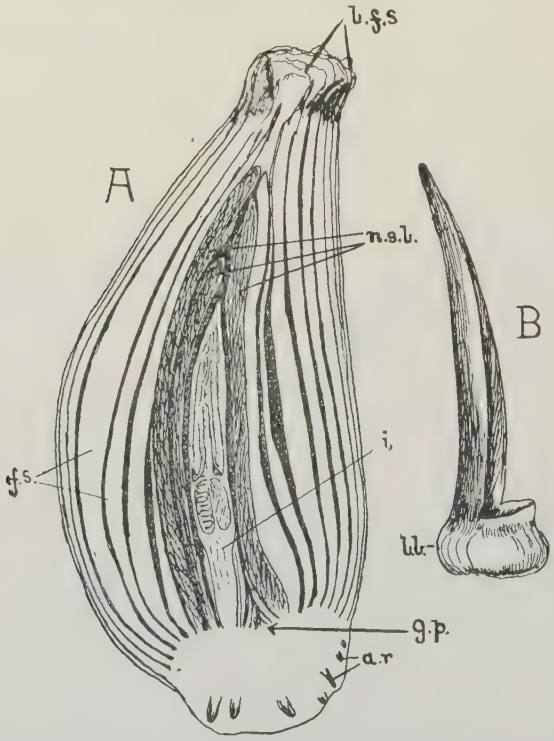


FIG. 93.—Structure of bulb of Narcissus (somewhat enlarged). A, In longitudinal section. B, Single foliage-leaf from the latter, showing the sheathing leaf-base. *a.r.*, adventitious roots; *g.p.*, growing point of bulb (*i.e.* apex of stem); *i*, inflorescence; *l.b.*, leaf-base which enlarges to form a bulb-scale in the next season; *l.f.s.*, enlarged bases (scales) of leaves of previous seasons; *n.s.l.*, young foliage-leaves of current year, whose bases will form fleshy scales in the next season.

drop, of several years in the case of the Narcissus). The foliage-leaves (*n.s.l.*) arise from the main axis which itself, however, remains quite short (*g.p.*), the flowering shoot (*i*) developing as an axillary branch from one of them. The terminal bud of

the bulb (*g.p.*) persists from year to year, producing each season two or more foliage-leaves and an axillary inflorescence, the whole enveloped in a membranous sheath; the bases of the leaves, as well as this sheath, swell up after flowering to form new fleshy scales for the next season's bulb. Other buds may be formed in the axil of the outermost scale and give rise to daughter-bulbs, whereby multiplication is effected. It will be noticed that the growth of the Narcissus-bulb takes place in a monopodial manner, whilst that of the Tulip is sympodial.

A last method of vegetative propagation is seen in the formation of so-called *bulbils*, *i.e.* small buds which become readily detached and the leaves of which, as in bulbs, are filled with food-reserves. In the British flora the best examples are the Lesser Celandine, some kinds of Wild Onion and the Coral-root. In the Wild Onion the bulbils take the place of flowers, whilst in the other two cases they arise in the axils of the foliage-leaves.

The foregoing description will have shown that vegetative reproduction is of widespread occurrence among flowering plants, although it is even more abundant among the lower forms of plant-life in which, moreover, it often takes place with great rapidity; thus, in the case of some Bacteria as many as thirty successive generations can be produced by mere division in the course of a single day. As contrasted with seed-production, the advantage of vegetative propagation lies in its simplicity, no complex union of different structures being necessary such as we shall see is involved in the formation of a seed (cf. p. 250). On the other hand, vegetative reproduction in most cases fails to bring about a wide separation of the offspring, which develop side by side and may thus mutually harm one another by competition, although in the case of propagation by runners or underground branches this disadvantage is somewhat minimised. An interesting method of removing the daughter-bulbs from the parent is seen in the case of the Tulip, in which they are often carried down into the soil by peculiar slender outgrowths known as *droppers*. In the Snowdrop again the main axis occasionally lengthens out, whereby the new bulb is conveyed some distance away from the parent.

All the storage-organs considered in this chapter are found at a certain distance beneath the surface, the exact depth ap-

pearing to be relatively constant in the same soil for each kind of plant. When such forms arise from seed, the seedlings are at first situated near the surface, but they are gradually brought to the appropriate depth by the agency of so-called *contractile roots* (*e.g.* in the Cuckoo-pint and Hyacinth). These are thick structures (Fig. 94 B and C) arising from the under

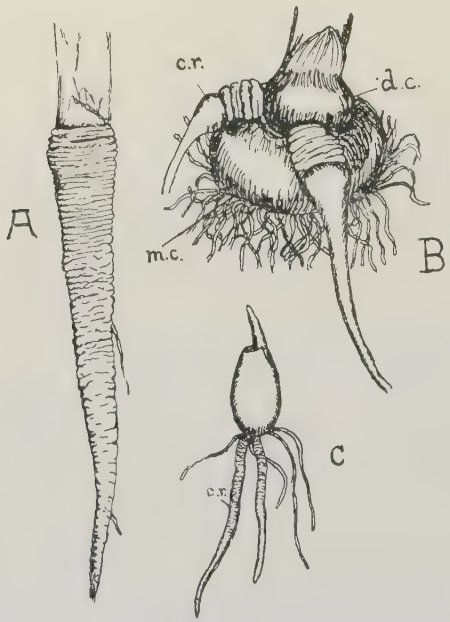


FIG. 94.—Contractile roots (A and B, natural size; C, slightly enlarged) A, Tap-root of Fennel. B, Crocus-corm. *c.r.*, contractile root; *d.c.*, daughter-corm; *m.c.*, mother-corm. C, One-year-old bulb of Broad-leaved Garlic with contractile roots (*c.r.*).

side of rhizome, corm, or bulb, and penetrating downwards into the soil. After their lower portions have become firmly anchored the upper parts (viz. those nearest the parent organ) contract, their surface thereby becoming markedly wrinkled, and as a consequence the structure from which they arise is dragged down to a lower level. A number of such contractile roots are produced each season until the correct depth has been attained. In some cases (*e.g.* the Crocus, Fig. 94 B) the new individuals

(*d.c.*) arise on the top of the old ones (*m.c.*) and so come to lie higher in the soil; in these the level is adjusted by contractile roots (*c.r.*) formed at the beginning of each season on the daughter-individuals. Some rhizomes appear to reach the right depth by growing downwards.

A similar contraction is exhibited by the swollen roots (p. 59) of the Dandelion, Dock, Fennel (Fig. 94 A), and other members of the Parsnip-family. The new leaves of the radical rosette formed above the old ones at the beginning of each season are thus pulled down in close contact with the soil.

We may conclude this chapter with a brief consideration of the principal kinds of food-materials stored up in the organs above noticed, extending our discussion to embrace also the reserves present in seeds (cf. p. 29). In a large majority of cases the food-substances consist in the main of *starch*, as can be proved by the Iodine-test. Starch always occurs in the form of solid grains of varying size and shape, which can be detected on examining with a lens a thin slice of a Potato stained with Iodine. In other cases, however (*e.g.* in the Solomon's Seal, the Carrot, and the Onion), *grape-sugar* (*glucose*) forms the main food-reserve and its presence can be recognised in the following way.

A number of thin slices of the organ concerned are placed in a test-tube and a small quantity of a solution of caustic potash (better with a little Rochelle-salt) poured over them, a few drops of copper sulphate solution being then added. Thereupon the whole is boiled, when almost immediately a yellowish-red precipitate of cuprous oxide is formed; this indicates the presence of grape sugar which has effected a reduction of the dissolved cupric to the insoluble cuprous oxide. The same reaction may now be repeated with slices of Grape or Apple, which give a similar result. The sugars in such fruits are not, however, of the nature of reserve-materials, but serve to attract animals which thus help to disseminate the seeds (cf. p. 287).

The grape sugar in all these cases is dissolved in the cell-sap (p. 108) and the same is true of other kinds of sugars, such as the *cane-sugar* which is the food-reserve of the Beetroot and the Sugar Cane. To demonstrate the presence of this sugar, slices must first be boiled in water to which a few drops of hydrochloric acid have been added. This serves to convert the cane into grape sugar, whose presence can then be shown in

the way above described; without the previous boiling, however, no precipitate is obtained with cane sugar.

In many members of the Dandelion-family (*e.g.* Dahlia, Salsify) another kind of dissolved food-reserve, known as *inulin*, is found. To observe this, a number of thin slices of a Dahlia-root are placed in methylated spirits which, after some little time, precipitates the inulin in the tissues as a number of small bright transparent bodies which disappear when the slice is treated with boiling water.

Starch, inulin, and the two kinds of sugars mentioned are the forms in which carbohydrates are most commonly stored up in plants, but the hard character of the endosperm (Date, Star of Bethlehem) or cotyledons (Lupine) of certain seeds is due to the storage of carbohydrate food-substance in the form of very strongly thickened cell-walls composed of *cellulose* (p. 135). None of these carbohydrates, except grape sugar, is directly utilisable by the plant; this is because solid starch and cellulose must first be rendered soluble before they can be transferred, and because inulin and cane sugar, though dissolved in the cell-sap, do not in this form pass readily from cell to cell. As a consequence all of these food-substances are converted into grape or other similar sugars, when they are about to be transferred for the use of growing parts.

Thus, when a seed of the Bean or Pea germinates or a Potato sprouts, the abundant reserve-starch gets slowly converted into soluble sugars which form the starting-point from which the more complex substances are built up (cf. p. 134). A similar change takes place in the foliage-leaves at night, when the starch which has accumulated during the day is converted into sugars and removed from the scene of its formation (cf. p. 135). It is obvious that some agency must be at work in bringing about these changes, since a so-called starch-solution (see Appendix XIX.) becomes converted into sugar at so slow a rate that it is almost negligible. On the other hand, by boiling, subsequent to the addition of a few drops of hydrochloric acid, the change into sugar is much accelerated; so that after some hours the solution no longer gives the characteristic blue colour with Iodine, whereas a sample of it will show the grape sugar reaction described above.

In the plant it is not an acid which brings about the change,

but a body of the class known as *ferments* (*enzymes*), the one concerned in the conversion of starch into sugar being known as *diastase*. This is formed in considerable quantity at the onset of germination in all starchy seeds and is readily obtained, for instance, from germinating Barley (the malt of breweries).[1] If some malt be ground to a fine powder (best done with the aid of a coffee-mill) and then shaken up thoroughly with water, a solution of the diastase is obtained. To eliminate other dissolved substances about a pint of methylated spirits is slowly added to a small amount (*e.g.* a fluid ounce) of the filtered solution; as a result the diastase is slowly deposited as an opalescent and flocculent precipitate. The clear solution above is subsequently poured away, and the precipitate filtered off from the remainder. On redissolving the precipitate in water a moderately pure solution of diastase is obtained. A small quantity of it is now added to a starch-solution and the rapid conversion into sugar noted.

Diastase is, however, not confined to germinating seeds, but is responsible for the change from starch to sugar wherever it is effected in the plant. Similar ferments bring about the conversion of the other carbohydrates into a suitable form. In the case of thick cellulose walls this process goes on very slowly and in consequence the period of germination is greatly prolonged, as is well seen in the Date. In the spring-time, when rapid conversion of the reserve-starch stored up in the woody parts takes place, large quantities of sugars are often carried up to the developing shoots of trees and shrubs in the water-current, so that the sap which exudes in "bleeding" (p. 109) often tastes quite sweet.

Apart from carbohydrates, however, other forms of food-reserves are found in plants; for instance, the *oils* and *fats* which are present in a considerable number of seeds (*e.g.* Castor Oil, cf. p. 32, Hemp, most nuts) and which, whilst again consisting of Carbon, Hydrogen, and Oxygen, contain much less of the last in proportion to Carbon and Hydrogen than in the case of a carbohydrate. These food-reserves are often of great

[1] The malt is obtained by allowing moistened Barley to germinate at a moderate temperature, after which the latter is raised so as to kill off the Barley, the conversion of starch into sugar continuing owing to the presence of diastase.

economic value (*e.g.* the use of nuts in the manufacture of margarine). They are readily recognised by the fact that they leave a greasy mark, if the contents of the seed be smeared on blotting-paper, this mark in many cases disappearing when the paper is soaked in methylated spirits or benzene.

The carbohydrates or fats in storage-organs are accompanied by more complex types of food-reserves which are nitrogenous and often of the nature of *proteids*. In the seeds of the Castor Oil or in the Brazil Nut, for example, large quantities of the latter are present in the form of small solid grains within the cells. Their presence can be recognised by the fact that a thin slice of the seed-contents takes on a deep yellow-brown colour some minutes after treatment with Iodine. Similar proteids are present also in the seeds of the Pea or Bean but, owing to the abundant starch, their presence cannot be detected in the way just described and another very characteristic proteid-reaction may be employed (see Appendix XX.).

A number of seeds of Pea or Castor Oil are pounded in a mortar and the mass is then shaken up thoroughly with water. The filtered solution, which now contains proteids, is boiled with the addition of one or two drops of nitric acid, whereupon a yellow colouration or a yellow precipitate is obtained. When ammonia is added the yellow colour or precipitate turns to a deeper yellow or orange tinge, and this change is a sure test for the presence of proteids.

It may be added that both fats and proteids are again not directly utilisable by the plant, but on germination first undergo change to an available form by ferment-action.

CHAPTER XIII

The Shoot in Relation to the Economy of Water

The ordinary annual or perennial herb grows under conditions in which the slight variations in the amount of water furnished by the soil are sufficiently compensated by changes in the width of the stomatal apertures (p. 116). The leaves of such plants are thin and flexible, which is due to the outer walls of the surface-skin being little thickened and only slightly impregnated with substances tending to prevent evaporation through the general surface. Such substances are, however, always present, constituting an outermost layer of the wall of varying thickness known as the *cuticle*.

When the latter is thin, as in the kinds of plants just mentioned, some slight evaporation takes place all over their surface; as compared with the transpiration through the stomates, however, this *cuticular transpiration* is generally quite negligible, except in immature leaves where the cuticle is not yet fully formed (cf. p. 172). The more strongly the cuticle is developed, the more leathery the texture of the leaf and the less the cuticular transpiration. Plants possessing such leaves (*e.g.* the Bilberry, Sea Holly) can consequently thrive in drier situations than the others and also, in many cases (*e.g.* the evergreens noticed in Chapter II.), are able to retain their foliage throughout the winter, when as previously stated absorption by the roots is often very slow (cf. p. 16).

Experiments with the potometer will have shown that transpiration is much less active from the shoot of an evergreen than from that of a deciduous plant (p. 119). By choosing leaves in which the stomates are restricted to the lower surfaces (*e.g.* Lilac, Black Poplar and Ivy), we can readily demonstrate that this is largely due to a difference in cuticular transpiration.

The ends of the petioles and the under sides of the laminæ are in each case covered with vaseline, and the two leaves are then suspended in a warm room ; it will be noticed that the Lilac-leaf withers much more rapidly than that of the Ivy. The experiment may now be repeated with unvaselined leaves, when the same result will be obtained. Similarly, if young and old leaves of a plant be compared, the young one is the first to wither owing to its thinner cuticle.

Plants which grow in a variety of situations show considerable differences in the thickness of the cuticle. Thus, the leaves of the Bracken or Bilberry growing on an open heath will be found to be thick and leathery, whilst those of the same plants growing in the moist atmosphere of a wood are thin and flexible.

When the foliage consists of broad thin blades, so that transpiration is rapid, the plant is classed as a *mesophyte* ; such forms are only able to thrive in localities in which water is plentiful, but they obtain large quantities of the necessary mineral salts in solution and consequently exhibit rapid growth. On the other hand, the plant with thick leathery leaves in which transpiration is correspondingly slow is an example of a *xerophyte* ; such a plant can exist in situations (*e.g.* a sand-dune, a heath) in which there is a deficient water-supply, but it receives a relatively small quantity of mineral salts from the soil, owing to the reduced water-current, and therefore grows but slowly.

Most deciduous trees and shrubs have mesophytic foliage, but by shedding this at the end of the season become xerophytes (*i.e.* able to exist with little water-supply), since the whole surface of the woody portion is covered with a layer of *cork* whose impermeability to water (and air) is well illustrated by its use for closing the mouths of bottles. In fact, even the leaf-scars (p. 73) are thus protected by a layer of cork which develops either before or after the leaf falls. In the case of perennial herbs an analogous winter-condition is attained by the dying down of the aerial shoots in the autumn (cf. p. 16).

Thickening of the cuticle is perhaps the simplest method of economising the water-supply and in this respect there are all transitions between the typical mesophyte and the typical xerophyte. In some cases a layer of *wax* coats the surface with a glaucous (p. 87) bloom (*e.g.* the Sea Holly, the Yellow Centaury, some fruits such as Plums) and thus aids the cuticle

in reducing transpiration. Dense coverings of *hairs* operate in the same way ; these hairs are outgrowths of the surface-skin and were already noticed in the Shepherd's-purse (p. 6), but are more obvious, for instance, in the Mullein, on the under sides of the leaves of the Lavender, as well as on the young blades of the Horse Chestnut (p. 97).

The effect of such a hairy covering is to impede the escape of damp air from the surface of the leaf, since the hairs prevent the removal by air-currents of the moisture given off in transpiration. The existence of such a partially saturated air-layer adjacent to the leaf-surface very materially reduces the rate of evaporation. The hairs themselves are either simple (as in the Groundsel, Fig. 95 A, the Cudweeds, the Mugworts) or richly branched (*e.g.* in the Shepherd's-purse, Fig. 4 C, the Mullein, Fig. 95 B, and Lavender, Fig. 95 C) or developed as small umbrella-like scales (*e.g.* the Sea Buckthorn, Fig. 95 G). Their efficiency as transpiration-checks naturally depends on how densely they clothe the surface of the plant. The appearance of the blade is greatly altered by the mode of arrangement of the hairs upon it ; when they are all placed parallel to one another the surface appears silky (as in the Barren Strawberry and Silver Weed), but when they are irregularly entangled it looks cottony (*e.g.* in many Thistles) or woolly (*e.g.* Mullein).

Many young leaves (*e.g.* Horse Chestnut, Plane) are closely beset with hairs which become separated or even fall off (Plane) as the blade expands, so that in the mature condition the latter appears almost glabrous (p. 87) and transpiration can go on freely. In the majority of cases the hairs appear white which is due to their being dead and containing nothing but air. Besides checking transpiration, hairs may also serve to screen the chlorophyll within the blade from too intense illumination (cf. p. 131) and by virtue of their air-content to reduce the passage of heat-rays to the leaf.

The maintenance of a layer of damp air above the surface of the leaf-blade is, as we have seen, an important method of checking transpiration, and this can be effected in other ways than by the development of a hairy covering. Thus, in many xerophytic leaves the stomata are depressed below the general surface,[1] so that a column of damp air accumulates above

[1] This fact can only be seen with the help of a microscope.

each, whereby a similar reduction in water-loss is effected. Again, the massing of the foliage in dense rosettes (seen in the Thrift, many Saxifrages, and very commonly in alpine plants) brings the transpiring surfaces into close contact, so that semi-saturated air accumulates in the spaces between them; moreover, such plants are usually of low growth, only sending up a vertical axis in the flowering season, and are therefore relatively little exposed to wind-currents.

The advantage of such massing together of the transpiring

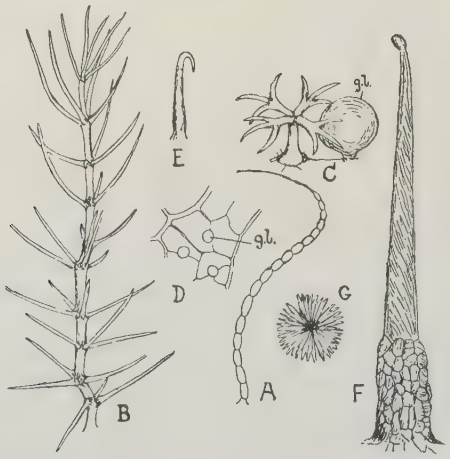


FIG. 95.—Types of hairs found on plants (all considerably magnified). A, Groundsel (simple hair). B, Mullein (branched hair). C, Lavender (branched and glandular hair, *gl.*). D, Black-currant leaf (glandular hairs, *gl.*). E, Hooked hair of Comfrey. F, Hair of Stinging Nettle. G, Scaly hair of Sea Buckthorn.

surfaces is well illustrated in the case of trees growing in exposed situations. New shoots that arise on the side of the crown sheltered from the prevailing winds develop normally, but those on the exposed windward side get cut off owing to excessive transpiration. In this way growth becomes more or less restricted to the leeward side, so that the familiar asymmetrical crown results.

The deciduous plant has been seen to meet the conditions of drought in winter-time by shedding its leaves, except for the scales enveloping the buds,—that is to say, the transpiring surface

becomes greatly reduced. A similar reduction, though less extreme, is exhibited by many xerophytes throughout the year. In the simplest case the foliage-leaves are of small size, but still carry on assimilation, as for instance in Conifers (*e.g.* Scotch Fir, Arbor-vitæ) and Club Mosses. Other xerophytes show a reduction of the leaves to mere scales, more or less destitute of chlorophyll, the assimilatory functions being transferred to the stem.

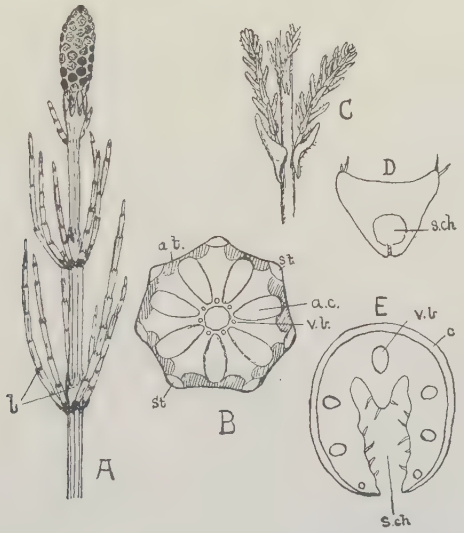


FIG. 96.—Reduction of the transpiring surface in xerophytes (Figs. A and C slightly reduced, the others considerably magnified). A and B, Horsetail Fern (switch-plant); B, stem in cross-section. *a.c.*, air-cavities; *a.t.*, assimilatory tissue of stem; *l*, scaly leaves; *s.t.*, strengthening tissue; *v.b.*, vascular strands. C, Small portion of plant of Heather. D, Cross-section of rolled leaf of same. E, Cross-section of rolled leaf of Sheep's Fescue. *c*, cuticle; *S.ch.*, chamber containing damp air; *v.b.*, vascular strands.

This is the case in the so-called "*switch-plants*," *e.g.* the Horsetail Ferns (Fig. 96 A) and the Broom. In the former the leaves constitute a whorl of connate scaly teeth (*l*) at each node, whilst the ribbed stems are green and in section (Fig. 96 B) show groups of assimilatory tissue (*a.t.*) opposite the shallow furrows in which the stomates are situated, the ribs being occupied by strands of strengthening tissue (*s.t.*). In the Broom

small green trifoliate leaves occur as well as scales, but the main assimilatory functions are here also performed by the stem. During the winter, after shedding its leaves, the Bilberry relies solely on its green stems and consequently becomes a switch-plant.

The transpiring surface is also in effect reduced by rolling of the leaves in such a way that the stomates come to lie within a chamber. Such *rolled leaves* are found in many heath-plants (*e.g.* Heather or Ling, Fig. 96 C and D), as well as in most xerophytic Grasses (*e.g.* Sheep's Fescue, Fig. 96 E). As the diagrams show, the edges of the blade are brought together so as almost to meet in the middle line (Fig. 96 D and E), the outer surface being covered with a thick cuticle (*c* in Fig. 96 E) and thus precluding cuticular transpiration, whilst the lower side with its stomates lines a cavity containing air, more or less saturated with water-vapour (*S.ch.*). The retention by young leaves, after emergence, of the folding exhibited within the bud (cf. p. 98) serves to reduce transpiration in a similar manner until the cuticle is fully formed.

In some of the Grasses concerned (*e.g.* Marram Grass (*Psamma*), Sheep's Fescue) the blade becomes more or less unrolled when the plant is receiving sufficient moisture, whilst a deficiency results in its closing up again. This is due to certain cells situated on the inner side, which, being very thin-walled, readily lose water when transpiration is excessive; thereby the inner surface contracts and the leaf rolls up, just as a sheet of stout cardboard curls towards a fire in front of which it is held. When these cells become turgid the inner side expands and the leaf opens, just as the curved cardboard flattens out if its inner surface is damped.

A peculiar type of xerophyte is seen in the Butcher's Broom (Fig. 98 B) and the Asparagus (Fig. 97), where, as in the switch-plants, the leaves are reduced to mere scales, whilst the assimilatory functions are taken on by specially modified branches known as *cladodes*; examples of this kind, though rare in Britain, are met with quite commonly in the desert-regions of the earth. In the Asparagus a tuft of narrow leaf-like branches, on some of which the flowers are borne (in reality a dwarf branch-system), arises from the axil of each scaly leaf (Fig. 97, *l*), whilst in the Butcher's Broom the cladodes arise singly and

are broad leathery leaf-like structures which, through a twisting of the base, are placed more or less vertically (Fig. 98 B, *cl.*).

Such plants appear to be anomalous, inasmuch as they substitute leaf-like branches for foliage-leaves, and we must suppose that in them the stems became more readily modified to xerophytic conditions than the leaves. A similar explanation probably applies to those cases in which the blade has become reduced and its functions taken on by vertically expanded

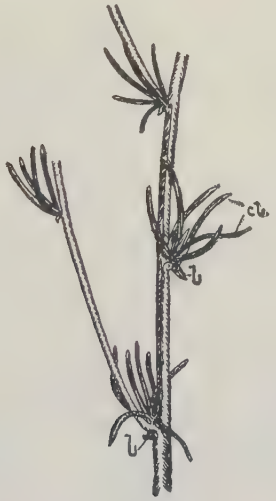


FIG. 97.—Small portion of a branch of the Asparagus with cladodes (natural size). *l*, scale-leaves on main stem; *cl.*, cladodes.

petioles (so-called *phyllodes*, well seen in species of Acacia, but not found in the British flora).

Other xerophytes exhibit a modification of their leaves or branches to form hard stiff pointed structures known as *spines*. These contain large quantities of thick-walled tissue (hence their tough consistency) and consequently very little transpiration takes place from their surface. The best example in the British flora is afforded by the Gorse or Furze (Fig. 99 D) in which both leaves and branches are spiny. That this habit is assumed as a protection against excessive transpiration is shown by the fact that plants grown in a moist atmosphere (*e.g.* a damp

greenhouse) produce few or no spines and develop normal flexible foliage-leaves, although of small size. The seedling

FIG. 98.—A, Small portion of branch of Barberry, showing the three-branched leaf-spines (*l.s.*) (natural size) ; the foliage-leaves arise from a dwarf-shoot (*d.s.*) in the axil of the spine. B, Branch of Butcher's Broom with cladodes (natural size). *cl*, cladode ; *f*, flower ; *l*, scale-leaves on main stem ; *s*, ditto on cladodes.

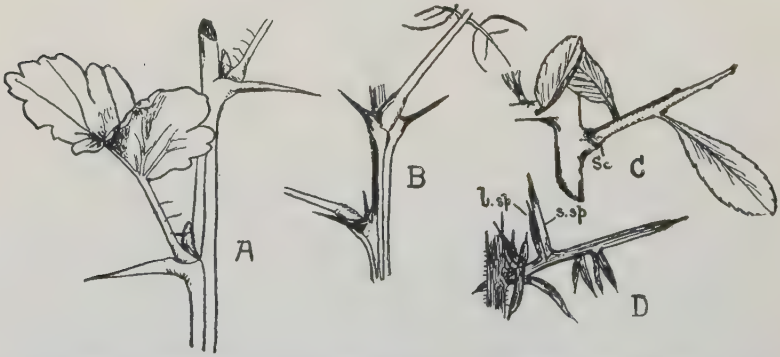


FIG. 99.—Examples of spinous plants (all figures natural size). A, Gooseberry (leaf-spines). B, False Acacia or *Robinia* (stipular spines). C, Sloe (stem-spines). *sc.*, leaf-scar. D, Gorse or Furze (leaf- and stem-spines). *l.sp.*, leaf-spine ; *s.sp.*, stem-spine.

of the Gorse (Fig. 100), moreover, does not immediately bear spines, these only appearing when the shoot has grown to some height above the surface of the ground ; this is probably due

to the air immediately above the soil being relatively moist, as compared with that at higher levels.

There are many other examples of spinous plants in our flora, in which the spines are not an obvious xerophytic adaptation, but for the sake of convenience they may be considered here. A good instance of *leaf-spines* is furnished by the Wild Barberry (Fig. 98 A, *l.s.*), where the leaves on the long shoots

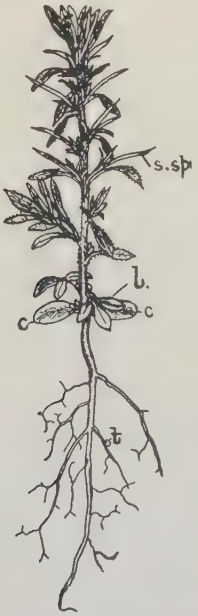


FIG. 100.—Seedling of the Gorse, showing transition to spines (natural size). *c*, cotyledons; *l*, first foliage-leaves; *s.sp.*, stem-spines; *t*, root-tubercle.

are replaced by three-branched spines, in whose axils arise dwarf-shoots (*d.s.*) bearing ordinary foliage-leaves and inflorescences. In the Gooseberry (Fig. 99 A) the spines which are simple or branched can be recognised on the summer-shoots as outgrowths from the leaf-base, whilst in the False Acacia (Fig. 99 B) they arise in pairs at the base of the petiole and are therefore modified stipules.

Stem-spines are seen, for instance, in the Sloe (Fig. 99 C),

the Hawthorn, the Spiny Rest-harrow, etc., and are recognised not only by their axillary position, but also by the fact that they often bear leaves. Finally, we may notice that in many plants the leaves themselves have spiny margins, as in the Holly, Sea Holly, Thistles, etc.

Spines have no doubt in most, if not in all, cases arisen as a modification to meet the need for reduced transpiration, but when they occur they are certainly of value to the plant in keeping off browsing animals and may even have become further developed in this connection. Thus, in the Holly the lower leaves almost invariably have spiny margins, but those near the top of the bush are usually without spines, differences that may be related to the relative ease with which they can be reached.

In speaking of cladodes and spinous branches we have had occasion to refer to them as modified structures, and other cases of modification will be considered in later chapters (see especially Chapter XVII.). The true character is invariably indicated by the axillary origin of the organs in question (*e.g.* the axillary position of the cladode in the Butcher's Broom, Fig. 98 B, or of the spine in the Sloe, Fig. 99 C), as also by the fact that they bear leaf-structures and occasionally flowers; thus, in the Butcher's Broom (Fig. 98 B) the upper surface of each cladode bears a small scale-leaf (*s*) in whose axil one or two flowers (*f*) appear in March or April. When the modified structure represents a leaf, its nature is apparent from the fact that it subtends an axillary branch or bud (Fig. 98 A) and is not itself subtended by a leaf.

All the devices for water-economy hitherto considered aim at a reduction of the amount of moisture transpired, but there is obviously a second method of providing against dry conditions, which is usually found in combination with the first. Thus, many xerophytes store up water in certain tissues and, when these represent a large part of the plant, the latter acquires a fleshy or succulent character. Such plants (*succulents*) lay up reserves of water, in times of rain, to be used during subsequent periods of drought and, as a general rule, either the leaves or the stem are employed for this purpose; in the latter case the leaves themselves are usually modified into spines.

The Stonecrops and Houseleeks (Fig. 101) afford good ex-

amples of leaf-succulents, whilst stem-succulents are scarcely represented in the British flora, but are well illustrated by the common Cacti. Such succulents can exist for a very prolonged period without external supply of water, during which they gradually shrivel more and more. Owing to their very thick cuticles they transpire very slowly and hence the moisture stored up within them lasts for a long period. Most of these forms have become so suited to dry conditions that their roots rot in a soil of average dampness.

A certain amount of protection from excessive transpiration in strong sunlight is obtained in a few plants by the leaf-blades assuming a more or less vertical position. In the simplest case they occupy this position permanently, as in the Iris and

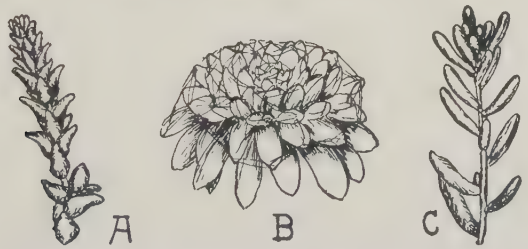


FIG. 101.—Examples of leaf-succulents (all natural size). A, Yellow Stonecrop or Wall-pepper. B, Houseleek (*Sempervivum arachnoideum*). C, White Stonecrop.

Gladiolus; the same applies to many cladodes and phyllodes (cf. above). The leaflets of the Wood Sorrel are often found, on a hot summer's day, more or less drooping as in the night-position (cf. p. 221 and Fig. 126), whilst those of the False Acacia under these circumstances become tilted upwards at an acute angle (*i.e.* a position opposite to the one assumed at night, cf. p. 91).

The so-called "Compass-plants" (*e.g.* the Prickly Lettuce) effect the same object in a different way. In a shady situation their leaves are spread out in the usual horizontal position, whilst in a sunny locality the blades are vertical with the edges facing north and south. The advantage of the upright position in all cases lies in the fact that the rays of the midday sun fall very obliquely on the blade, so that their heating effect (cf. p. 123) is much diminished. In "Compass-plants" the

north and south position of the blade means that its edge is always presented to the sun at the hottest part of the day.

In the ordinary horizontally placed lamina the upper and lower surfaces differ considerably in structure (cf. p. 129 and Fig. 68), and such a leaf is therefore described as *dorsiventral*; the difference in structure is probably related to the fact that the upper side is more exposed to the sun than the lower. When the blade is permanently vertical, however, both sides receive an equal amount of sunlight and in such cases there is no difference in structure between the two surfaces (*e.g.* Iris). A slightly different type is seen in the practically cylindrical leaves of some xerophytes (*e.g.* Rushes, Onion) in which the construction of the blade is identical all round.

Many xerophytes, especially Conifers among British plants, produce large quantities of readily evaporating resins or ethereal oils (p. 137), whose vapour, for instance, is very noticeable on entering a Pine-wood. The presence of such vapours renders the air less permeable to the heat-rays of the sun and the plants concerned are therefore in some measure protected. Whilst the Conifers form these substances within their tissues, other plants (*e.g.* the Lavender, Rosemary and similar sweet-scented herbs) produce them in so-called *glandular hairs* (Fig. 95 C and D) developed principally on the surfaces of the leaves. In many cases, however, such glandular hairs form substances whose purpose may merely be to render the plant distasteful to animals.

The modifications of the shoot discussed in the preceding pages all aim at harmony between the plant and its surroundings; so that a comparison of different kinds of plants growing under similar conditions, even in widely separated regions of the earth, will reveal much in common (*e.g.* the plants growing in loose sand). Moreover, even in the individual itself mesophytic and xerophytic features may be united (*e.g.* in deciduous trees), bearing a definite relation to the circumstances under which the various parts exist. So too the seedling does not necessarily resemble the adult (cf. the Gorse), and the Buttercup of the meadow differs essentially from that of the pond or ditch. Finally it should be added that, though some of these modifications vary with the conditions of growth, others are more or less fixed and tend to put a limit to the variety of circumstances under which the plants possessing them can thrive.

CHAPTER XIV

The Breathing Process of the Plant

The life-processes of every living organism are always associated with a chemical break-down, the outward evidence of which is an absorption of Oxygen and a giving out of carbon dioxide. We have previously (p. 12) pointed out that this respiration goes on at all times in the plant, but is masked during the daytime by the more active assimilatory process in which the gaseous exchange is reversed. As a consequence the volume of Oxygen evolved is less than that actually formed in photosynthesis, since part of it is used for breathing; similarly, the carbon dioxide produced in the latter process is not liberated, when the plant is exposed to light, owing to its being used for purposes of assimilation as soon as it is formed. Hence an evolution of carbon dioxide from a green plant can only be demonstrated in darkness.

It is probably for the most part carbohydrate-substance that is broken down in the process of respiration in plants and, taking grape sugar as an example, we can in a general way illustrate the chemical change involved by the following equation :—

$$\underset{\text{Grape sugar.}}{C_6H_{12}O_6} + \underset{\text{Oxygen.}}{6O_2} = \underset{\text{Carbon dioxide.}}{6CO_2} + \underset{\text{Water.}}{6H_2O}.$$

From this it will be seen that the volume of carbon dioxide given out is equal to that of the Oxygen taken in, and that water-vapour is simultaneously produced. This evolution of water-vapour in the course of the breathing process is a familiar fact in animals, but is difficult to demonstrate in plants owing to transpiration going on at the same time.

One method of demonstrating the occurrence of respiration was described on p. 12, but this experiment only proved the

removal of Oxygen. If, however, we plunge a glass rod which has been dipped into lime-water into the jar containing the living plants, the lime-water rapidly turns milky, a sure indication that a considerable amount of carbon dioxide is present; in the control-jar no such rapid change is observed. The same experiment, if performed with plants lacking chlorophyll, can be carried out in the light with similar results.

Another way of showing that plants respire is to place a number of germinating Peas in a flask provided with a tight-fitting rubber cork, through the single hole of which a glass tube twice bent at right angles is inserted (Fig. 102). Suspended

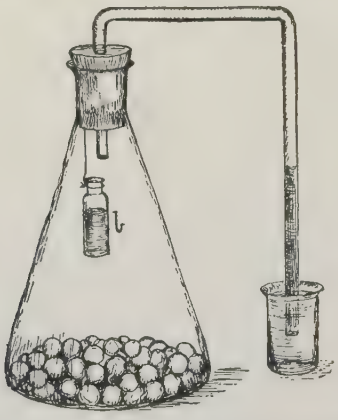


FIG. 102.—Apparatus to demonstrate that germinating Peas give off carbon dioxide in the process of respiration. For description, see text.

in the flask by a cotton thread is a small bottle (*b*) containing a concentrated solution of caustic potash, whilst the free arm of the tube dips into a tumbler of water. The carbon dioxide evolved by the Peas, in place of the Oxygen taken in, is absorbed by the potash and as a consequence a reduced pressure is produced within the flask, so that a column of water rises in the tube, as shown in the figure (see note on p. 189).

Since every living cell of the plant must breathe, it is necessary that there should be free access of Oxygen to all parts, and this is effected by a continuous system of air-spaces opening to the exterior by way of the stomates (p. 116) and lenticels (p. 74).

The experiment described on p. 115 (Fig. 62 B) has already illustrated the connection between the stomates and the air-spaces of the leaf (cf. Fig. 68 B, *a.s.*), as well as the continuity of the latter with those of the stem. The fact that the lenticels are apertures giving access to the same system can be shown by placing woody twigs, in which the cut ends have been sealed with melted paraffin-wax, in warm water, when large bubbles of air will be seen to arise from the lenticels. If the stem of a plant is cut off just above the root and the latter immersed in hot water, bubbles of air will be given off from the cut surface

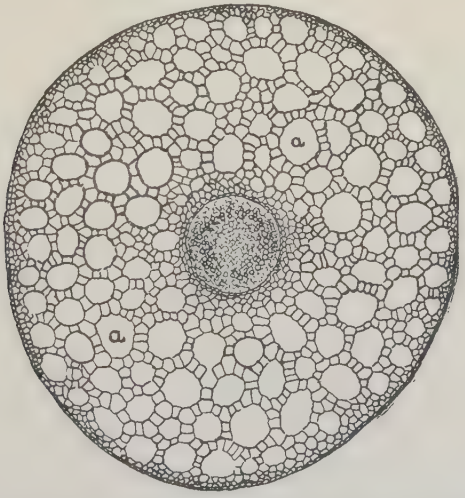


FIG. 103.—Cross-section of the stem of the Mare's-tail, a water-plant (considerably enlarged). *a*, air-spaces.

for some little time, thus showing that the air-spaces of the root are likewise continuous with those of the stem.

Air-spaces can be readily seen in cross-sections of the stem of any water-plant (*e.g.* the Pondweeds, the Bulrush, the Mare's-tail, Fig. 103, the flower-stalks of the Water Lily), where they are of exceptionally large size for a reason to be given later (p. 332). The air-system of plants serves, not only for the access of Oxgyen, but also for the escape of the carbon dioxide formed in respiration and of the water-vapour which is transpired to a limited extent from all the living cells.

Since Oxygen is essential for normal respiration, its absence leads to a cessation of all vital processes. This stoppage is most easily recognised in the case of growth and it has, for instance, already been shown (p. 25) that when Oxygen is absent seeds fail to germinate. The method previously employed is, however, open to the objection that water, even when unboiled, is not the natural medium for the growth of a land-plant. It is therefore more satisfactory to place a few (*e.g.* ten) soaked seeds in two *large* closely stoppered jars, in one of which is suspended a small tube containing pyrogallate of potash. The latter is obtained by dissolving pyrogallic acid in water and adding an excess of caustic potash (which should not be done until immediately before the experiment is started). This solution absorbs Oxygen very energetically (as a result of which it takes on a brown colour) and consequently the seeds in the jar containing it will fail to germinate, whereas those in the control do so in the normal manner.

The plant, however, unlike the ordinary animal, is not immediately killed by absence of Oxygen, although under these circumstances all the normal life-processes are arrested. When there is no Oxygen in the surrounding air, plants carry on a modified breathing process known as *anaerobic respiration*, during which carbon dioxide is evolved as under ordinary conditions. To demonstrate this, we first peel the coats off a number of soaked Peas, since air may be included between the testa and the cotyledons. A small test-tube is then filled with Mercury and inverted into a shallow dish containing the same substance (Fig. 104), whereupon the Peas are passed under the mouth of the test-tube and allowed to float to the top of the Mercury. At first they are only partly visible, but gradually they become more and more exposed till, after some hours, they lie freely in a gaseous atmosphere which, displacing the Mercury, has collected at the top of the test-tube (Fig. 104). If sufficient Peas are employed and the experiment is left for about twenty-four hours, nearly the whole test-tube will become filled with gas. This can be shown to be carbon dioxide by dipping a glass rod with lime-water into it.

During anaerobic respiration carbohydrates are probably again broken down, but not as completely as in the normal breathing process, so that, apart from carbon dioxide, certain

still relatively complex substances (*e.g.* alcohols) are produced. These, as they gradually accumulate, poison the living cells of the plant and thus sooner or later bring about death. If, before this has occurred, the plant is restored to a normal atmosphere containing Oxygen, it will in most cases recover and resume its ordinary life-functions.

The respiratory process of plants, like assimilation (cf. p. 134) and other functions, is markedly influenced by temperature,

FIG. 104.—Apparatus to demonstrate that germinating Peas give off carbon dioxide even in the absence of Oxygen, *i.e.* carry on anaerobic respiration. Description in the text.

being slight when the latter is low and steadily increasing as it rises. A very slow rate of breathing is further exhibited by dormant structures containing little water, *e.g.* dry seeds and many Lichens and Mosses (such as grow on tree-trunks) which remain alive, even when apparently dried up.

Our consideration of respiration has shown that it entails a breaking down and loss of substance. Since under ordinary circumstances assimilation is so much in excess of respiration, this loss is scarcely noticeable, but if we prevent assimilation by placing a green plant in the dark it is easy to show a decrease

of organic substance. Two lots of about five Peas (of approximately equal size in the two cases) are weighed, whereupon they are separately soaked and placed to germinate, the one lot in the dark, the other in the light. After about a fortnight the dry weight (p. 124) of both lots of seedlings is determined and compared with the weights of the original seeds,[1] when it will be found that the seedlings grown in the dark have lost considerably, while those grown in the light have gained.

The equation on p. 183 shows that the substances produced in respiration (viz. carbon dioxide and water) are the same chemically simple ones, from which the green plant builds up carbohydrates in the course of photosynthesis. It was pointed out in dealing with the latter process that a considerable amount of energy was required to accomplish this change (p. 132), and this energy remains in a latent condition until it is again liberated in equivalent amount by the breaking down of the carbohydrates. There is consequently a setting free of energy during respiration, and this is manifest in many actively growing structures which often breathe with such vigour that a portion of the energy liberated takes the form of heat.

Thus, if a funnel be filled with germinating Peas or young flower-heads of the Dandelion, packed round the bulb of a thermometer, the latter will soon record a higher temperature than one in a control in which cotton-wool is substituted for the plant-material. Both experiments are best covered with bell-jars to eliminate the effect of air-currents.

The energy of respiration furnishes the driving power of the plant's machinery, supporting not only life itself, but all the vital functions as well, and we can therefore understand why the latter cease when normal respiration is arrested. In anaerobic respiration a certain amount of energy is likewise liberated, though few or no vital processes are manifested. It may be mentioned, however, that, particularly among the Bacteria which are responsible for many virulent diseases (*e.g.* Anthrax, Cholera, Typhus), there are organisms which not

[1] It would be better to compare with the *dry weight* of the original seeds. This can be approximately estimated by determining the dry weight in percentages of the original weight for a number of Peas, and working out the dry weight of those employed in the experiment by simple proportion.

only ordinarily exist in the absence of Oxygen, but to whom this gas, except in minute quantities, is actually a poison. Hence the importance of ventilation in the prevention of disease.

A process somewhat comparable to anaerobic respiration is seen in alcoholic fermentation, which is effected by certain microscopic plants (*e.g.* Yeasts and Bacteria) and in which there is likewise a production of carbon dioxide and alcohols. In these cases, however, the alcohol is formed by breaking down of sugary solutions outside the plant and does not involve the rapid death of the organism which produces it.

Note.—Another way of performing the experiment on p. 184, which will give a more rapid result, is to suspend the Peas in a small basket made of wire-gauze, and to use as an absorbent, for the carbon dioxide, soda lime with which the bottom of the flask is covered. To avoid the effect of rapid changes in temperature the flask as a whole can be placed in a large vessel of water.

CHAPTER XV

The Growth of the Plant

One way in which the energy of respiration is employed is in the process of growth, during which part of the food-material produced in the course of nutrition is used in building up new tissues. All growth comprises three distinct phases, viz. (i) the formation of new units by the division of the cells of the growing points (cf. pp. 7 and 49), (ii) the enlargement of the new units (p. 50), and (iii) the modification of the same to perform the different functions which they fulfil in the life of the plant. Of these the second is the only phase of growth visible externally and constitutes what is known as growth in popular parlance.

The *growing points*, which are situated at the extreme tips of the shoot (Fig. 49, *g.pt.*) and just behind the caps in the root (cf. p. 48), consist of numerous small cells which during growth undergo repeated division. Some of the units thus produced become gradually converted into mature cells and lose their power of division, whilst others retain it and continue to serve as the growing point. Apart from such apical growing points, the stems of some plants exhibit a similar tissue situated between portions which have already attained to maturity. Thus, in Grasses such *intercalary growing points* are found just above each node, and in members of the Pink-family at the nodes themselves; they are recognisable by the soft texture of the stem in these regions. The intercalary growing points in the plants mentioned only come into play, however, when the shoots are prostrated through rain or wind and are subjected to the one-sided influence of gravity (see p. 209).

It may be added that, inasmuch as the petiole is the last part of the leaf to be formed (p. 98), the growth of the latter is in its later stages also intercalary. Moreover, the increase in thick-

ness of woody stems (p. 102) and the formation of cork (p. 172) are due to the active division of tissues situated within the mature body of the plant.

The restriction of growth to definite points is a marked feature of contrast between the growth of plants and of higher animals. A further distinction is seen in the continual formation of new organs (leaves, branches, roots) from the growing points of plants, whereas in the ordinary animal the number of organs remains constant after the embryo-stage is over.

It has been pointed out that in roots elongation is restricted to a very short portion (p. 50), whilst in stems it is spread over a much greater length (p. 80), but if we adopt means to compare the rate of increase of different parts of the elongating zone we shall find that it is not uniform. This can be done in the case of roots by repeating the experiment described on p. 49 (Fig. 26) and noting the exact amount of growth in length between each pair of marks. As we have seen, the intervals near the tip of the root will have elongated little, but, as we pass progressively farther from the apex, the intervals become wider and wider until they reach a maximum width; beyond this they again exhibit a gradual decrease till we come to the mature zone, where no growth in length has taken place (see Fig. 26 B, p. 49).

The result of this experiment can be more easily realised if a curve (graph) be constructed in the following way (Fig. 105): On a horizontal line equal divisions are marked off, equivalent in number to those upon the root, and from each mark a vertical line is raised, whose length is proportional to that of the corresponding segment on the root. By joining up the ends of the verticals (as in Fig. 105) a curve is obtained which rises to a summit and then falls again.

As we pass away from the tip of the root we come to older and older segments (*i.e.* intervals between two marks), and in the above experiment therefore we are comparing the amount of elongation in segments of different ages. This shows us that the cells of the newly formed segments elongate but slightly at first, but, as they get older, grow in length more rapidly until when they approach maturity their rate of elongation again decreases. This gradual rise and fall in the rate of elongation is spoken of as the *grand period of growth* and, since the cells

in a given transverse plane exhibit the same rate of increase, the successively older segments epitomise the changes of the individual units.

A similar grand period is exhibited by growing stems and can be well seen in seedlings. If we mark the plumule of a Runner Bean in the way previously described for the root (p. 49 and Appendix V.), but over its whole length, we shall find after a day or two that the intervals have elongated over a much wider zone than in the case of the radicle; they show, however, the same gradual increase and decrease as we pass

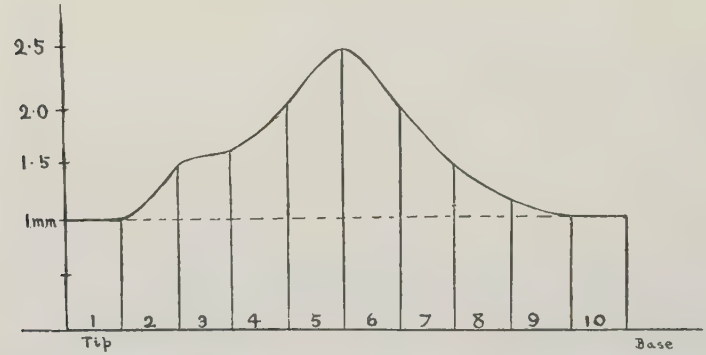


FIG. 105.—Curve illustrating grand period of growth, constructed from radicle shown in Fig. 26 B. The tip and base of the radicle are indicated.

backwards from the tip (Fig. 106). It is instructive to mark the radicle of the same seedling for the sake of comparison.

In developing shoots the nodes usually cease to grow soon after they are formed, the later elongation being restricted to the internodes, so that growth in length takes place in a number of separate regions, *i.e.* it becomes segmented. The ultimate length of the internodes is generally not equal, those near the base and the top of each season's growth being relatively short, whilst the intervening ones often show a progressive increase in length towards the middle. This is well seen in many herbaceous plants (*e.g.* Bedstraws, Woodruff), as well as in the shoots of many trees and shrubs (*e.g.* Apple, Laurel, Poplar); the following are given as examples :—

LENGTHS OF SUCCESSIVE INTERNODES (IN MILLIMETRES) ALONG A ONE-YEAR'S SHOOT.

Apple . .	1	2½	3	7	12	20	30	30	30	40	25	20	21	10	8	5	3
Laurel . .	4	7	16	16	18	21	20	13	3	...	...	...	...	...	...	...	...

If we require to measure the rate of growth of an entire organ we can adopt one of several methods. The simplest is,

FIG. 106.—Experiment to demonstrate region of growth in plumule of Runner Bean (about two-thirds natural size). At the beginning of the experiment the marks were all at equal distances from one another.

of course, direct measurement, the observations being made at regular intervals (*i.e.* daily, every two days, etc.). This is practically the only method applicable to roots which for this purpose are grown behind glass in the box described on p. 54. Since the amount of growth is mostly very slight, an increase of accuracy is obtained, if we employ means to magnify it. For this purpose we use an instrument known as a *growth-lever* (Fig. 107) which can be readily constructed.

It is composed of a light wooden lever[1] (*l*), with two unequal arms, working on a metal pivot (*p*) which consists of a fine nail that passes through a piece of tin (*t*) doubled over the lever at this point (see the small inset in Fig. 107). A small strip of lead *w* (*e.g.* from the covering of a tea-packet) is wrapped round the short arm of the lever, so as nearly to balance the weight of the long one. The pointed end of the lever works over a graduated cardboard arc, the divisions of which show the actual amount of movement of the short arm (Appendix IX.). The

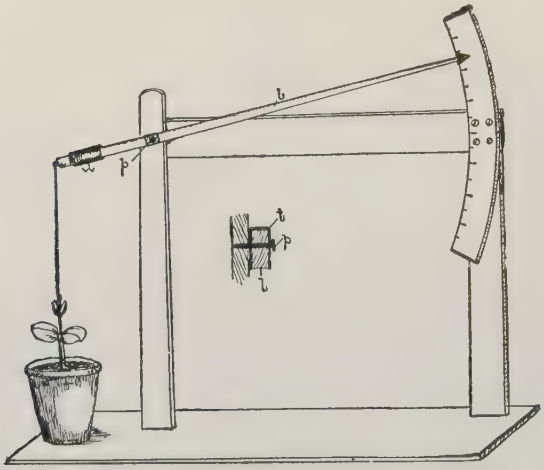


FIG. 107.—Simple form of growth-lever. For description, see text. The small figure in the middle explains the mode of attachment of the lever to the upright support.

growing tip of the plant to be experimented with, is surrounded with a small pad of cotton-wool, round which one end of a thread is then firmly tied, the other end being attached to the short arm of the lever in such a way that the pointer is at the top of the scale. As the plant grows the pointer will sink and thus the amount of elongation can be noted.

It is sometimes convenient to measure the hourly growth of a plant, and for this purpose we require an instrument known as an *auxanometer*. Several types of the latter can be purchased

[1] This can be made from an ordinary thin garden-stick by planing down the surface.

(see Appendix XXI.), but the following instrument (Fig. 108) has certain advantages over the others and moreover is cheaper. The flat wooden base bears (i) an adjustable pillar on the top of which a light wooden lever works, (ii) an upright, to the back of which a wooden arm is pivoted about an inch from its top. The arm bears at its upper end a frame which securely holds a square piece of glass; the lateral movement of this arm is restricted by two adjustable screws. At the lower end of this arm is a projection whose end bends downwards at right angles. A cheap clock is fixed face upwards (Fig. 108) behind the movable arm in such a position that the minute-hand in its

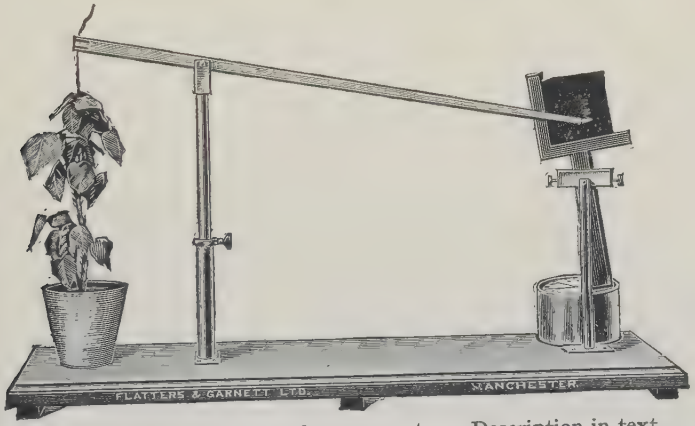


FIG. 108.—Simple form of auxanometer. Description in text.

movement will come into contact with the projection. The position of the clock is such that the minute-hand after pushing aside the arm some little way ultimately loses contact with it, so that it swings back to its original position; this takes place automatically, owing to the glass plate being placed slightly to one side at the top of the arm. The pointed end of the lever just touches the surface of the glass plate.

To prepare the instrument for use, the glass plate is removed from its frame and covered with a uniform layer of soot by holding it over the smoky flame of burning camphor. The tip of the plant is attached as before by a cotton-thread to the short arm of the lever. As in the case of the growth-lever, the growth of the plant leads to a gradual fall of the

pointer which consequently traces out a vertical line on the sooted surface. Every hour, however, the glass undergoes a lateral movement, whereby the pointer is caused to make a horizontal mark, so that if the experiment be continued for some time we get a series of horizontal lines, the intervals between them representing the magnified hourly growth.

Both the growth-lever and the auxanometer will enable us to determine the conditions influencing growth. Thus, by both means we can establish that elongation is more rapid at night than during the day (provided the temperature remains approximately uniform), although the auxanometer is somewhat more helpful in this connection. The marks made by the pointer will be found to be farthest apart after midnight and nearest together after midday, whilst in between a perfect gradation connects the two extremes. This shows us that there is a *daily period* in the growth of the plant, due to the alternation of light and darkness. With the growth-lever, by taking readings in the morning and in the evening on successive days, it will also be found that the total growth at night is greater than that in the day.

The increased rate of elongation in the dark is well illustrated by plants (*e.g.* seedlings, sprouting Potato-tubers, etc.) which are allowed to grow in total absence of light. Under these conditions, apart from the non-development of chlorophyll (cf. p. 10), the plant exhibits an exceptional elongation of the internodes, whilst the leaves remain of small dimensions (Fig. 109 A); such plants are said to be *etiolated*. Even dull light has a similar effect and many herbaceous forms (*e.g.* Willow-herbs) exhibit longer internodes in the shade of a woodland than when growing in the open. Similarly the herbs are often appreciably taller on the shady than on the sunny side of a hedge. This acceleration of growth in darkness is of great advantage in nature, especially in the case of shoots which commence their development underground (*e.g.* plumules and shoots of herbaceous perennials), since by virtue of this feature they reach the surface rapidly.

In plants possessing rhizomes or root-stocks the absence of light induces exceptional elongation of the petioles, a fact which is made use of in the commercial production of Celery, Rhubarb and Sea Kale. A further interesting effect of absence of light can be observed in certain rosette-plants (*e.g.* House-

leeks) in which well-marked internodes, separating the radical leaves from one another, are produced under these circumstances, so that the plant acquires quite a different habit.

Apart from its influence on the rate of growth, the intensity of the light also in some cases affects the extent of development of plant-organs. Most of the buds within the crown of shade-casting trees, for instance, fail to develop, whereas at the margin

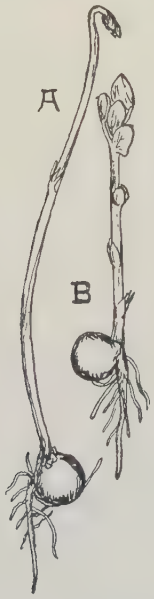


FIG. 109.—Seedlings of the Pea (about three-quarters natural size), normal (B) and etiolated (A). Both are of the same age.

the majority of them give rise to branches; and we may even find that the crown is denser on the side facing south than on that facing north. Similarly many herbaceous plants (Pignut, Yellow Dead-nettle, etc.) flower little, if at all, when growing in the deep shade of a wood, but do so profusely after the latter is coppiced. If the leaves of two plants of the same kind growing respectively in the sun and in the shade (*e.g.* Dog's Mercury, Enchanter's Nightshade) be compared, it will be found that the blades of the former are smaller and thicker than

those of the latter (cf. Fig. 110). A similar difference will be found between the exposed and shaded leaves of the same plant (*e.g.* the Beech).

In the above experiments it was stated that, in order to observe the accelerating influence of darkness, it is necessary to keep the temperature approximately constant. As can be shown with the growth-lever, this is due to the fact that heat and cold exert a profound effect on growth, as on other functions (cf. pp. 134 and 187), inasmuch as plants grow slowly at a low temperature, whilst as the latter rises the rate of elongation increases until a degree of heat is attained which is unsuitable

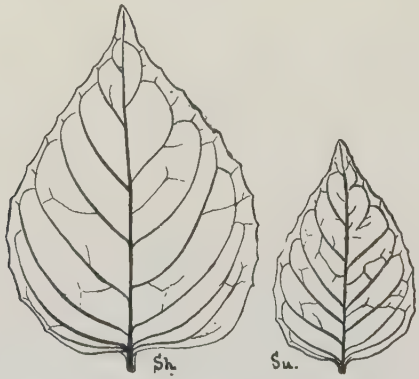


FIG. 110.—Sun- (*Su.*) and shade-leaves (*Sh.*) of the Enchanter's Nightshade (about one-half natural size).

for further existence. Since the temperature at night is usually lower than in the day, the tendency to more rapid growth at night is masked in nature.

The effect of temperature-conditions upon growth is well illustrated by several observations on plants in their natural environment. Thus, whereas some exhibit vigorous growth already in the early spring (*e.g.* Dog's Mercury, Lesser Celandine, Elm, Willow), others have to await a higher temperature and do not become active till the end of April or May (Ash, Beech, Horse Chestnut). Many plants (*e.g.* Lily of the Valley) moreover can be induced to grow and flower out of season by exposing them to a warm temperature (*i.e.* forcing them). The northward and southward extension of plants of warmer regions

again is limited by the lowest temperature at which they can grow ; thus, certain Palms can exist in the open in the south of England, but not further north. In our conservatories many tropical plants are cultivated by supplying them with a suitable temperature, but in some cases they fail to flower, and this is probably due to the light of our latitudes being too weak.

Apart from illumination and temperature, the most important condition influencing growth is the supply of Oxygen, but this has already been considered fully in the last chapter (p. 186). An adequate supply of moisture and nutritive material is also essential.

The rate of growth of most plant-organs is so slow that we have found it necessary to employ means to magnify it ; and to this general statement there are but few exceptions. The filaments of the stamens (cf. p. 7) of Grasses remain quite short until the pollen is ripe, but then a very rapid elongation takes place, amounting, in the case of the Wheat, to nearly 2 mm. per minute. The shoots of some tropical Bamboos exhibit a similar, though somewhat less rapid, growth. The size attained by different kinds of plants, although variable within certain limits, is nevertheless approximately constant. On the one hand, we have very minute forms (*e.g.* Duckweed, Common Whitlow-grass); on the other, tall-growing trees and, amongst annuals, such types as the Sunflower.

We have still to consider the third phase of growth (cf. p. 190) during which the internal structure is modified until the mature condition is reached. Up to the conclusion of growth in length no prominent thickening of cell-walls takes place and the organ relies mainly on the turgid character of its cells for support (cf. p. 102). It is usually not until elongation is over that the woody strands become hard and thick-walled and that the other special strengthening tissues described on p. 99 are developed. In the course of their modification a considerable number of the cells of the plant die and lose their protoplasm, the walls at the same time frequently undergoing chemical change ; it is to this latter that the hard character of the wood and the impermeability of cork are due.

In most herbaceous plants practically no change takes place after maturity, but in woody perennials, as we have seen, a slow growth in thickness, both of stem (p. 102) and root (p. 57) con-

tinues as a result of the annual addition of new rings of wood. Owing to this gradual increase in thickness the protective surface-skin is burst and consequently ceases to be effective. Its place is taken by a layer of cork, the value of whose impermeable qualities we have already considered (p. 172). As the plant gets older, successive layers of cork are produced, each on the inner side of the preceding one, whilst the earlier-formed layers crack, as did the original skin, and constitute the bark (Fig. 61 A, *bk.*).

FIG. 111.—Apparatus for the demonstration of circumnutation. For description, see text.

If we examine closely the growing apex of a shoot we shall find that it does not move upwards in a straight line, but describes a slightly irregular course, somewhat spiral in its general character. This *circumnutation* is, however, generally not apparent unless we employ special means to demonstrate it, as, for instance, the apparatus shown in Fig. 111. This consists of a sheet of glass held horizontally by vertical supports at the four corners, the plant whose growth is to be observed being placed underneath it and the successive positions of the apex marked from above by affixing pointed strips of gummed paper

to the glass (see Fig. 111). For this purpose a small rod *a* (*e.g.* a knitting-needle) is fixed to one of the four supports, so that its tip is situated vertically above the main stem and about an inch from the apex of the plant. Each strip of gummed paper should always be so affixed that its point forms a straight line with the tip of the rod *a* and the apex of the plant, a certain magnification of the movement being thereby obtained.

Good material for observing circumnutation is furnished by the plumule of the Runner Bean (before its tip bends over into a horizontal position), as well as by any uncurved tendril. This phenomenon (which is exhibited by stems and roots alike) is due to one side of the apex growing more rapidly than the opposite one, the zone of more rapid growth continually shifting its position round the circumference of the stem. As a result the growing tip is not straight, but exhibits a slight, often scarcely recognisable curvature, in one direction or another.

In plants the growth of one organ is often materially influenced by that of another, so that if the one is favoured or arrested, the other exhibits a reduction or promotion. We have already met with several instances of such *correlation*. Thus, in etiolated plants the poor development of the leaves (p. 196) is associated with the greater growth of the stem. If the terminal bud is removed from a shoot, laterals which would otherwise remain dormant are caused to sprout (cf. p. 78); some of the dwarf-shoots often elongate, when the apex of the main shoot is cut off (p. 79). Similarly, after removing the tip of the tap-root in a Bean or Pea, one or more of the lateral roots assume a vertical position and take its place. In those forms, moreover, in which extensive vegetative propagation obtains, reproduction by seeds is generally rare, a correlation plainly shown by the Lesser Celandine and many cultivated bulbous plants.

The effect of an injury to any living part of the plant is to cause the surrounding cells to undergo active division, whereby the wounded surface sooner or later becomes covered up with a new growth. When a branch of a tree is removed by a clean cut, new tissue gradually develops from the edge of the exposed surface forming a protecting rim which covers in the sap-wood. A similar stimulation to growth is seen in those cases in which injury due to Insects or Fungus-pests leads to the formation

of so-called *galls* (Fig. 112). In Insect-galls the special growth results from the laying of an egg or eggs by the female beneath the surface-skin and, in the same species of plant, different kinds of galls may be produced by different insects (*e.g.* Oak-apple gall, Cushion-gall, Fig. 112 C, Button-gall, Fig. 112 B, Bullet-gall, etc., all on the Oak). The abnormal growth known as the Witch's Broom is due to various fungal pests which lead to an exceptional branching of the attacked part, examples being commonly seen on the Cherry, Birch, and Elm.

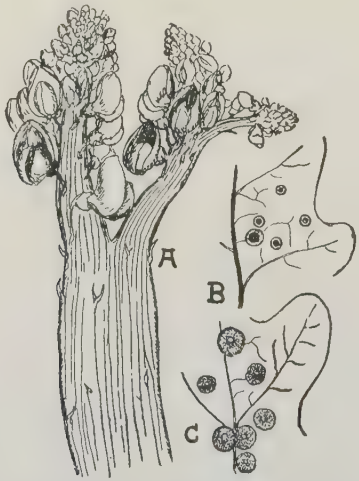


FIG. 112.—A, Abnormal specimen (monstrosity) of the Runner Bean inflorescence in which the branches have combined to form a flat axis. B, Button-gall of Oak. C, Cushion-gall of Oak. (All figures about two-thirds natural size.)

Occasionally plants exhibit unusual forms of growth which in many cases are probably a result of exceptional conditions of life. Such *monstrosities* find expression in various ways, most commonly in a combined development of the different branches of a shoot-system, so that the whole forms a flat structure (Fig. 112 A). A similar process leads to the production of the Coxcomb and the Cauliflower, both of which are monstrosities which have become more or less permanently fixed by cultivation. Double flowers seen in many cultivated plants furnish other examples of monstrosities.

The stimulation to growth as a result of wounding is made use of in the propagation of plants by cuttings (cf. p. 57), as well as in the processes known as *budding* and *grafting*, which are much employed in Rose- and Fruit-culture. In budding (Fig. 113 A and B) a shield-shaped piece of the bark, extending in as far as the wood and bearing a bud (Fig. 113 A), is cut off from one plant and inserted beneath the flaps produced by making a T-shaped incision in the bark of the stock (Fig. 113 B). In grafting (Fig. 113 C–F) a portion of a twig is removed from the one plant (the *scion*) and its tapered lower end (Fig. 113 C and E) is pushed into a V-shaped slit in the wood (Fig. 113 D)

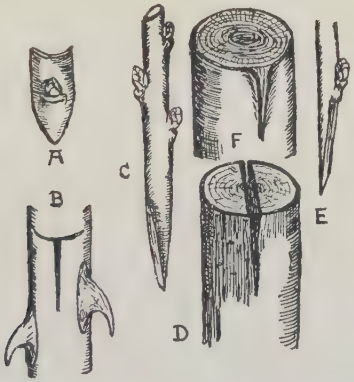


FIG. 113.—Budding and grafting. A and B, Budding. *A*, bud; *B*, stock. C–F, Grafting. C–D, Cleft-grafting. E–F, Slip-grafting. *C* and *E*, scion; *D* and *F*, stock.

or under the bark of the stock (Fig. 113 F), so that the wood and bast of the latter are in contact with those of the scion. In both methods the cut surfaces are protected from infection and drying up by covering them over with grafting wax. The two adjacent surfaces in both cases grow together so that a complete connection results.

Grafting and budding are usually only possible between related types of plants. The general effect of the process in the case of Fruit-trees is to bring about earlier and more abundant fruit-production. In the case of Rose-culture budding is specially advantageous as enabling florists to perpetuate forms which do not produce seeds.

CHAPTER XVI

The Direction of Growth as affected by Outside Influences

As a result of elongation during growth the positions of the growing points are continually altering, *i.e.* they exhibit a forward movement which, as we have seen (p. 200), does not take place in a straight line. In all such cases the slight curvatures occurring during circumnutation ensue in the natural course of events and are not due to external influences or *stimuli*. One, however, frequently meets with other growth-movements leading to curvatures which can be definitely ascribed to outside agencies. The effect of the latter is to produce a change in some specially receptive portion of the plant, which ultimately results in a curvature in the zone of elongation.

Attention has already been called to the influence of gravity in inducing the upright growth of the ordinary shoot (p. 18) and the downward growth of the main root (p. 53), the phenomenon being referred to as *geotropism*. The experiments already described sufficiently illustrate these general facts, and it need only be added that an organ which curves in the direction of the force of gravity is said to be *positively*, whilst one which curves the opposite way is said to be *negatively* geotropic.

It might be thought that the downward curvature of a horizontally placed root was due to its own weight, although the negative behaviour of the shoot makes this unlikely, as well as the absence of curvature in a dead root. Even when a certain amount of resistance has to be overcome, however, roots will nevertheless be found to curve downwards when placed horizontally. This may be shown by filling a shallow cup with a solution of gelatine and, after this has solidified, fixing seedlings to corks (wedged on to the edge of the cup) in such a way that their radicles lie horizontally on the surface of

the gelatine. The curving roots will be found subsequently to push their way into the latter, whereas similar seedlings which have been killed by brief immersion in boiling water remain horizontal.

So long as the shoot and root are situated with their axes parallel to the line of action of gravity, no curvature takes place, *i.e.* we have a condition of equilibrium. As soon, however, as either occupies any position other than the vertical, this state of equilibrium is upset and curvature sooner or later takes place until gravity again acts *equally on all sides*. The condition for a geotropic curvature in an ordinary shoot or root is therefore a one-sided action of gravity. If a seedling is placed horizontally in the dark and then slowly rotated on its own axis,

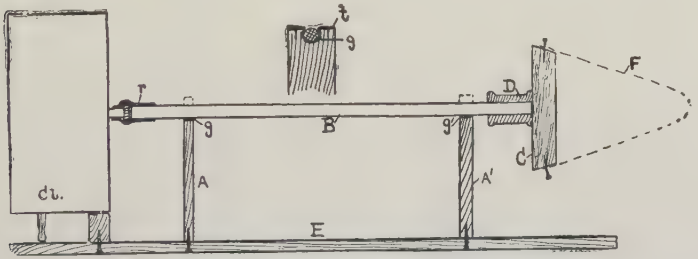


FIG. 114.—Simple form of klinostat. The small figure at the top shows a front view of the upper part of one of the supports A or A^1. For further description, see text.

it will of course be exposed to such one-sided influence; as a result of the rotation, however, all sides in succession will be subjected for an equal period of time to this one-sided stimulus and consequently no curvature will be observed.

To perform this experiment we use an instrument known as a *klinostat* (Fig. 114, see also Appendix XXII.) which can be made cheaply in the following way: To the centre of a large (4-inch) cork C is firmly nailed a cotton-reel D, into the hole of which a piece of thick glass tubing B is wedged. The glass tubing (about 14 inches long) is supported near each end by a wooden upright (A and A^1, each 3 inches high), the two being firmly attached to the wooden base E. The two uprights are provided with a groove (g and g^1) which is just deep enough to receive the tube and is lined with a narrow strip of tin (t),

so as to give a smooth bearing (see small figure at top of Fig. 114). The free end of the tube *B* is attached to the *central* spindle at the back of a cheap clock (*cl.*) with the help of a piece of rubber tubing (*r*). When the clock is wound up, the hourly rotation of the central spindle brings about a similar rotation of the cork. The seedlings are pinned to the surface of the latter in a horizontal position (by means of blanket-pins passing through the seeds). It is best previously to cover the surface of the cork with a layer of damp cotton-wool and, afterwards, to pin to the edges of the cork a sugar-loaf-shaped bag (*F*) made of thick blotting-paper which is kept moist by occasionally

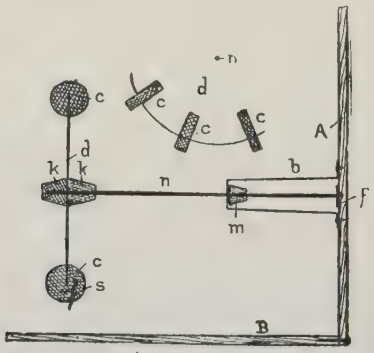


FIG. 115.—Diagram to explain construction of a simple centrifugal apparatus (modified from Osterhout). For description, see text. The upper figure shows a small part of *d* from the surface.

sprinkling it with water. In carrying out this experiment control-seedlings should be laid horizontally beside the klinostat.

A somewhat similar force to gravity, and moreover one with which we can more easily experiment, is centrifugal force. This finds expression in the tendency of a heavy body to fly outwards, when swung round in a circle at the end of a piece of string. The influence of this force on the direction of growth of the ordinary root and shoot is exactly like that of gravity, *i.e.* when attached to the edge of a wheel, which is rapidly rotated in the vertical plane, the root of a seedling assumes a position pointing outwards and the shoot one pointing inwards along a radius of the wheel. The experiment can be easily performed with the following simple *centrifugal apparatus* (Fig. 115; modified from Osterhout).

This consists of a circular piece of tin *d* (6 to 8 inches in diameter), such as can be readily cut with a pair of strong scissors out of the side of an ordinary biscuit-tin. A number of flat slices (*c*, about quarter of an inch thick) are cut from some 1½-inch corks and fitted firmly into eight slightly narrower slots, cut at equal intervals (*c*, *c*) into the margin of *d*. The centre of *d* is attached with the help of two corks (*k*, *k*) to one end of a knitting-needle *n*, the other end of which is supported by a piece of tin (*b*), shaped as in the figure, and allowing free movement of the needle. The tip of the latter revolves freely in the perforated tin plate *f* and is prevented from escaping from this lower bearing by the cork *m* through which it passes. *b* is firmly screwed to the wooden base *A*, to which a second base *B* is attached at right angles. When the instrument rests on *B* the wheel *d* rotates in the vertical, when on *A* in the horizontal plane.

For use seedlings (*s*) with straight plumules and radicles (Appendix IV.) are pinned in any position to the right *or* left-hand side of each cork, all being on the same side in a given experiment. Thereupon a spray of water from a tap is directed (with the help of a rubber-connection and a piece of bent glass tubing) against the *unoccupied* sides of the corks, so that the whole apparatus works like a water-wheel, the rapidity of rotation depending on the strength of the spray. If the wheel be made to revolve in the vertical plane, the result will be that the seedlings are exposed equally on all sides to the action of gravity and will consequently respond to the centrifugal force alone, assuming the position described in the last paragraph but one.

When the wheel is rotated horizontally, however, the seedlings are exposed to the one-sided influence, both of gravity and centrifugal force, and will be found to take up a position with the radicles pointing outwards and downwards, and the plumules inwards and upwards; as the rapidity of rotation is increased, both radicles and plumules become more nearly horizontal. The ultimate position of the two parts of the seedling in this case is a result of the combined action of the horizontal centrifugal force and of the vertical force of gravity. Thus, they come to lie at an angle which represents the position of equilibrium between these two forces. Such experiments not only show that centrifugal force affects the different parts of the

plant in the same way as gravity, but also that the two can act simultaneously.

Our consideration of creeping shoots, rhizomes, and lateral roots has shown that there are organs which respond neither positively nor negatively to gravity, but are in a position of equilibrium when more or less at right angles to its line of action, the same is the case with the horizontal branches of trees, and all such structures are said to be *diageotropic*. We have already seen (p. 54) that, if the lateral roots of the first order are shifted from their customary position, the growing parts curve until they form the same angle with the horizontal as before. The position occupied by these laterals probably depends to some extent on the presence of the main root, since removal of the latter causes one or more of the laterals to grow vertically downwards (cf. p. 201). In the case of rhizomes, planting in an inclined position leads to a curvature in the growing zone until the apex again lies horizontally.

A given organ does not always show the same response to gravity in different stages of its development. A good example is afforded by the Poppy (Fig. 116) in which the upper part of the flower-stalk is positively geotropic before the flower opens (*a*), diageotropic during the process of opening (*b*), and negatively geotropic when fruit-formation begins (*c* and *d*). Similarly, many rhizomes (*e.g.* the Solomon's Seal) are diageotropic, but their tips become negatively geotropic prior to the formation of the overground shoots.

If a seedling, in which plumule and radicle have been marked in the way described on p. 49, is placed horizontally in a dark box (cf. p. 53), it will be found that the curvature after twenty-four hours has in both cases taken place approximately in the region of maximum elongation (Fig. 117). Moreover, it will be noticed that both the extreme tip and the older part of each organ have remained almost straight. It can, however, be shown, in the case of the root, that this region of curvature is not the part in which the influence of gravity is first felt. If about a millimetre be cut off the tips of the radicles of a number of seedlings which are then placed horizontally (as in the experiment described on p. 53), no curvature of these radicles will be observed until new tips have developed, whereas control-seedlings behave in the normal way. Though this experi-

ment is open to the serious objection that the amputation of the tip may impair the bending capabilities of the root, more elaborate experiments support the conclusion that in the case of the root the power of perceiving a one-sided action of gravity resides in the apex. The impression which is here received must therefore be transferred in some way or other to the zone of elongation. It may be added that a similar localisa-

Fig. 116.—Flower-buds, flowers, and fruit of the Poppy, showing the successive positions (*a–d*) of the flower-stalk in successive stages of development (about one-half natural size).

tion of the perceptive power has also been demonstrated in certain shoots.

In referring to the intercalary growing points of Grasses, etc., it was stated that these only come into play when the shoot is laid prostrate (p. 190). In fact, whereas in most plants, when the stem becomes horizontal, the older part remains prostrate and only the actually growing part becomes erect, the whole shoot in Grasses soon assumes an upright position under these

circumstances. This is due to the fact that, when horizontal, the intercalary growing points are stimulated to growth which is more active on the under than on the upper side (Fig. 118).

The ordinary erect shoot has been seen to respond to one-

Fig. 117.—Experiment to demonstrate region of geotropic curvature in the plumule of a Runner Bean placed horizontally.

sided light by curving more or less markedly towards it (p. 17, Fig. 7 B), so that it affords an example of *positive heliotropism*. Aerial roots (*e.g.* Ivy, Fig. 31) and the tendrils of the Virginia Creeper and Vine furnish the commonest instances of *negative heliotropism*; a few subterranean roots (*e.g.* Mustard) are,

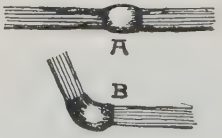


Fig. 118.—Intercalary growing points of a Grass, diagrammatic. A, Condition when first laid horizontally. B, Condition after a geotropic curvature has ensued. The swollen portion in each case marks the intercalary growing point.

however, also influenced negatively by one-sided light, although the majority appear to be unaffected.

For exact experiments on heliotropism it is best to employ a dark chamber of the type shown in Fig. 119; any long wooden box (which should not be less than 2 feet in length and about

1 foot broad by 1 foot high) will serve the purpose. This is made light-tight and painted black inside to prevent reflection. A small slit-shaped piece (about quarter of an inch wide and 5 to 6 inches high) is cut out of one of the ends of the box and a piece of board nailed on either side to increase the depth of the slit (see Fig. 119); the opposite end is hinged and serves as a door for introducing and removing plants.

In open spaces in nature light and gravity act together in producing the upright growth of the ordinary shoot, but at the edges of dense thickets and in hedges, where one-sided light comes into play, positive heliotropism is stronger than the negative geotropism, so that the shoots grow out towards the light. With the help of the dark chamber, it can be shown

FIG. 119.—Dark chamber for experiments in heliotropism. Description in text. The arrow indicates the direction of the light.

that the relative effect of the two influences varies in different plants; thus, the shoots of some (*e.g.* Pea) assume an almost horizontal position, whilst others curve to a less extent (*e.g.* Cress, Runner Bean), showing that they are more strongly affected by gravity.

That erect shoots do not curve, when uniformly lighted on all sides, is shown by every-day observation, as well as by the fact that no curvature takes place when a plant is rotated on a klinostat at right angles to the source of light, since each side is then in turn equally illuminated. If we mark the plumule of a seedling at equal intervals and then expose it to one-sided light in the dark chamber, it will be found that, as in the case of geotropic curvatures, the bending ensues in the region of maximum elongation.

Another analogy between the two kinds of phenomena is

seen in the existence of plant-organs which respond to the influence of light by taking up a position more or less at right angles to its direction. Such *diaheliotropism* is most strikingly exhibited by ordinary dorsiventral foliage-leaves and is responsible for the fixed light-position, assumed by the blade during development, a feature which is specially noticeable in the case of leaf-mosaics (cf. p. 84). There are, however, leaves which grow vertically (*e.g.* Iris) as a result of their being negatively geotropic.

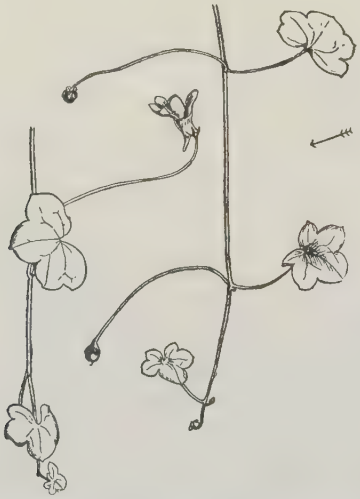


FIG. 120.—Change of heliotropic response in the flower-stalks of the Ivy-leaved Toadflax. The arrow marks the direction of the light.

A further similarity between heliotropism and geotropism lies in the change of heliotropic response exhibited by the flower-stalks of some plants. Thus, in the Ivy-leaved Toadflax (Fig. 120), very common on old walls in many parts of England, the flower-stalks bend towards the light (*i.e.* are positively heliotropic), but during the development of the fruit they curve away from it (see right-hand figure); in this way the ripening fruits are carried in the direction of the wall, so that the seeds are often shed in its crevices.

The power of perceiving one-sided light has also been shown in some cases to be restricted to certain regions, a fact which

can be demonstrated in young seedlings of Canary-grass in which the leaves of the plumule have not yet burst through the protective sheath. The tips of some are covered with small caps (Fig. 121, *c*), each about half an inch long and made by twisting silver paper round the point of a pin, whilst others (Fig. 121) are left uncovered. The whole pot is then placed in the dark chamber above described (Fig. 119). After about twenty-four hours the uncovered seedlings will have bent in the usual way towards the light, whilst the others have remained straight. The perceptive power is therefore in this case localised in the

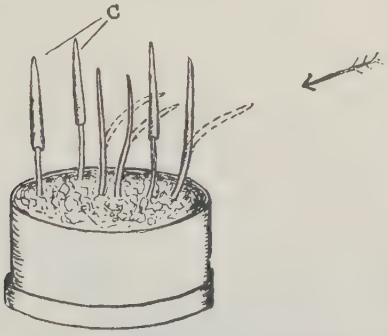


FIG. 121.—Experiment to demonstrate the localisation of light-perception in young seedlings of the Canary-grass. The arrow shows the direction of the incident light. *c*, caps of silver paper. The positions occupied by the uncovered seedlings at the end of the experiment are indicated by dotted lines.

upper part of the plumular sheath and, as in the geotropic curvature of roots, there must be a conduction of the stimulus to the region in which bending takes place.

We have already seen (p. 54) that a one-sided distribution of moisture produces a positive growth-curvature in roots, a phenomenon known as *positive hydrotropism*. This was demonstrated by growing seedlings in dry soil receiving its water-supply only by way of a porous flower-pot (Fig. 29), but a second method is shown in Fig. 122. A small wire sieve is filled to the depth of about half an inch with damp sawdust in which Cress-seeds are sown, the whole being then covered with blotting-paper which is kept wet. After this the sieve is suspended in

moderately moist air at an angle of about 45°, whilst a second similar apparatus is hung up horizontally. When the radicles of the Cress-seedlings emerge through the meshes of the sieve they will be found in the case of the sloping one to curve through a right angle, so that they again reach the damp sawdust (Fig. 122 *r*). This is due to the vertically growing radicles, on entering the relatively dry air below the sieve, being nearer to the moist surface on one side than on the other, and hence the necessary conditions for a hydrotropic curvature are realised. On the other hand, in the horizontal sieve, no such curvature is observed, since all sides of the radicles are equally stimulated by the moisture.

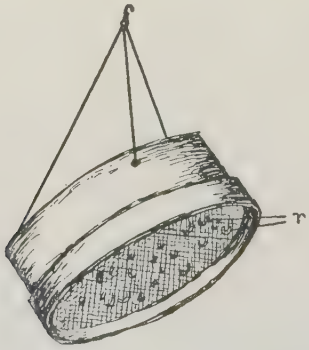


FIG. 122.—Experiment to demonstrate hydrotropism in roots. For description, see text. *r*, the curved radicles.

In nature hydrotropic curvatures are rarely seen except in the case of the finer branches of the root-system, but they are of considerable value in carrying these rootlets into regions of greater moisture. Negative is much rarer than positive hydrotropism and has been observed only in lower forms of plant-life.

Our study of the various growth-curvatures has shown that there is a certain parallel between them, especially between geotropism and heliotropism. In both cases there are organs which respond positively, others which respond negatively, and still others which place themselves at right angles to the directive influence. Further, in all cases the curvature ensues in the zone of elongation, somewhere about the region of maximum growth in length, and is due to the convex side elongating

more rapidly than the concave. In certain organs, moreover, we have seen that perception takes place at a point remote from the region of curvature and that consequently a conduction of the impression must occur.

The previous pages also show that the same stimulus may produce a totally different effect in different cases (*e.g.* gravity causes roots to curve towards the earth, shoots to curve away), so that there is obviously no definite relation between the cause of the impression and the type of effect produced. Moreover, we have seen that in certain cases a given organ responds in a different way to the same agency in various stages of its development (*e.g.* flower-stalks of Poppy and Ivy-leaved Toadflax).

Though a nervous system is absent in plants, these phenomena are analogous to nervous response in animals where likewise perception, the conduction of the impression, and reaction follow successively upon one another. Thus, if your finger touches a hot body, the muscles that move your hand away are situated in the arm—that is to say, at some little distance from where the pain was perceived.

CHAPTER XVII

Further Examples of Plant-Movements

Certain plant-organs exhibit growth-curvatures which are a result of direct contact with some foreign body and thus differ materially from those discussed in the preceding chapter. The commonest examples of such curvatures are furnished by *tendrils* (cf. p. 20), whose varied nature will, however, best be considered in the first place.

In most cases such tendrils are modified leaves or parts of leaves, as is seen in many members of the Pea-family, as well as in the White Climbing Fumitory and *Cobæa scandens*, a common greenhouse climber. In the Pea-family one or more leaflets of the usually pinnate blade become modified to serve as tendrils, the consequent reduction of assimilating surface being often compensated by the enlargement of the stipules and the production of green wing-like expansions by the stems and petioles; all of these features are well illustrated by the Sweet-pea (Fig. 123 B). In extreme cases (*e.g.* the Meadow Vetchling, Fig. 47 D) the whole blade is replaced by a single tendril, the very large stipules doing all the assimilatory work of the leaf. In seedlings of the plant just mentioned the lower leaves not infrequently possess small blades with relatively small stipules, the latter becoming larger in the upper leaves as the blade becomes reduced.

In the Climbing Fumitory the ultimate segments of the compound leaves are similarly replaced by tendrils, the tips of which are provided with a claw-like hook giving an easier grasp on the support; in *Cobæa* much the same structure is seen. The tendrils in all these cases are recognised as modified leaflets by the fact that they form part of a compound leaf (cf. p. 88). Where the whole blade is modified, as in the Meadow Vetchling,

the presence of an axillary bud betrays the foliar nature of the tendril. In a few plants (*e.g.* Old Man's Beard or Clematis, Canary Creeper) the leaf-blade remains unmodified, but the petiole acts like a tendril and entwines the support.

Branch-tendrils are relatively rare, the only example in the British flora being afforded by the White Bryony (Fig. 10); other instances are the tendrils of the Vine, the Virginia Creeper, and the Passion-flower. The plainest case is seen in the last-named plant, in which the simple tendrils definitely arise in the axils of the leaves, so that their branch-nature is manifest.

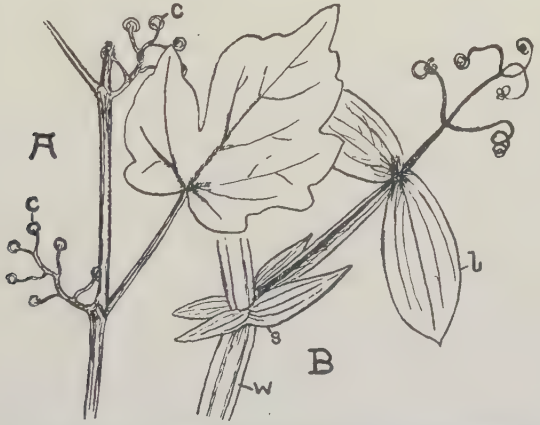


FIG. 123.—Tendrils of A, the Self-climbing Virginia Creeper (*Ampelopsis Veitchii*), and B, of the Sweet-pea (natural size). *c*, attaching cushions; *l*, unmodified leaflets; *s*, stipule; *w*, winged stem.

In the Vine and Virginia Creeper (Fig. 123 A) the branched tendrils arise at each node, on the side of the stem opposite to that bearing a leaf. This is due to the fact that each segment of the stem ends in a tendril which is bent over to one side, the growth of the main axis being continued by the axillary bud between the tendril and the leaf situated opposite to it, so that the whole stem is a sympodium (cf. p. 77).

In the White Bryony (Fig. 10) the exact nature of the simple tendrils is still doubtful; they arise together with a short branch (Fig. 10 B, *br.*), and frequently an inflorescence as well, from the axils of the foliage-leaves. Some regard the

tendrils as a modified first-leaf of the short branch, whilst others look upon it as a second branch developed in the leaf-axil. In this connection it may be mentioned that the occurrence of more than one bud in the axil of a leaf may be seen also in other plants (*e.g.* some Willows).

The tendrils or their branches, when young, are almost straight and constitute flexible structures composed of soft turgid tissue. At this stage their growing tips exhibit a very pronounced circumnutation (cf. p. 200) which materially increases their chances of coming into contact with a support. If this occurs, the side of the tendril opposite to that touched is stimulated to grow more rapidly, whilst that in contact with the support continues to grow at the same rate as before. This brings about a curvature of the tip of the tendril (cf. Fig. 10 A) and, as a consequence, new parts of it come into touch with the support and thus receive a fresh stimulus; moreover, the resulting curvature is not confined to the part actually in contact, but also affects adjacent parts of the tendril. In this way more and more of the growing tip becomes wound round the support, so that a firm grasp is obtained.

After this the part of the tendril between the parent-plant and the support gradually coils up into a close spiral and, since both ends of the tendril are fixed, the coils of this spiral of necessity exhibit a reversal at some point or other (Fig. 10 B). In this way an elastic spring-like connection with the support is developed, so that the risk of the plant's being torn away by gusts of wind, etc., is diminished. Soon after its attachment the tissue of the tendril begins to thicken and harden, so that it loses its soft flexible character and becomes firm and tough. Tendrils which fail to reach a support wither away and sooner or later generally drop off. It may be added that, where climbing is accomplished with the aid of sensitive petioles, the mechanism is exactly the same as in tendrils, although the effect of contact does not extend beyond the part in touch with the support.

The effect of a contact-stimulus can be imitated by gently stroking the under surface of a White Bryony tendril with the finger for about a minute. A curvature almost immediately becomes apparent and is generally very pronounced before long. As a matter of fact the changes leading to the curvature

of a tendril depend, not upon the actual contact, but upon rubbing against some foreign body. This has been proved by placing tendrils in contact with a support and ensuring the absence of all vibration, when no curvature is observed. Tendrils, moreover, are not stimulated by contact with fluid bodies, so that the impact of rain-drops is without effect.

The negatively heliotropic tendrils of the Self-climbing Virginia Creeper (*Ampelopsis Veitchii*) exhibit quite a different method of attachment to the support. The tips of their branches swell up into little cushions (Fig. 123 A, *c*) which, on meeting a solid body (*e.g.* a wall), cling to it by the production of a sticky substance and then, as a result of the contact-stimulus, gradually flatten out to form sucker-like discs which adhere very tenaciously to the surface. In the ordinary Virginia Creeper and the Vine the tendrils mostly function in the usual way, but should their tips come into contact with a firm surface they develop similar cushions which subsequently form adhesive discs.

The mechanism for encircling the support in stem-twiners (p. 21) is totally different from that found in tendrils, as is readily seen by the fact that no amount of stroking of a twining stem will produce any response. It seems probable that a peculiar action of gravity plays some part in this case, since stem-twiners can only coil round a more or less vertical support and lose their power of twining, when rotated on a klinostat. Furthermore, if a Runner Bean for instance, which has already wound round a support, is kept in an inverted position, some of the last-formed coils untwine and commence to wind in the opposite direction (Fig. 124).

The direction of twining, as seen from above, is usually constant for any given kind of stem-climber, taking place either from left to right (*i.e.* clockwise, as in the Hop, Fig. 11, Honeysuckle, and Black Bindweed) or from right to left (*i.e.* counter-clockwise, as in Convolvulus and the Runner Bean), but the Woody Nightshade which is an occasional climber sometimes twines in one direction and sometimes in another. Among British plants the Honeysuckle is the only woody twiner, but in the jungles of the Tropics numerous larger forms known as lianes are common.

Before leaving climbing plants it may be recalled that lack of the power of self-support has led to the adoption of a scramb-

ling habit by some plants (p. 20) or to the utilisation of adventitious roots for attachment to a prop (*e.g.* the Ivy, Fig. 31, and many tropical climbers). Climbers are often a marked feature on the shady side of a hedge where, owing to the rapidity with which they can reach a well-lighted position, they have the advantage over the other non-climbing herbs.

FIG. 124.—Effect of inversion on the twining stem of the Runner Bean. The soil is prevented from falling out of the pot (not shown in the figure) by a covering of cardboard.

We may now return to a further consideration of movements resulting from contact-stimuli. The curvature of the tentacles of the Sundew after an insect has been entrapped (cf. p. 150) is a case in point, although it may in part be due to a chemical influence. We here have a good example of the transference of the stimulus since, after the particular tentacles bearing the insect have curved inwards, other tentacles not in contact with it follow suit.

Similar movements due to contact-stimuli, but differing from those hitherto noticed in not depending upon unequal growth of the two sides of the curving organ, are seen in the stigma of the Monkey-flower (Musk) and in the stamens of the Common Barberry. In the former case the stigma consists of two flat spreading lobes (Fig. 125 A, *s*) which, on being touched (*e.g.* by the tongue of a pollinating insect, cf. p. 269), close together in the way shown in Fig. 125 B. The six stamens of the Barberry-flower project outwards, so that their anthers are some distance from the stigma, but, when any foreign body (*e.g.* an insect) comes into contact with the bases of the filaments, the stamens thus stimulated spring up into a vertical position, thereby covering the insect with a shower of pollen. In both of these

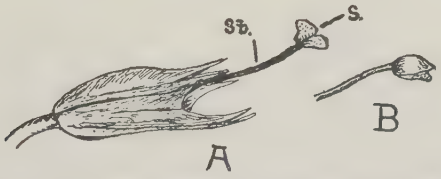


FIG. 125.—Response of the stigma of the Monkey-flower to contact-stimuli. A, Normal position. B, With the two lobes of the stigma closed together, after a stimulus has been received. *s*, stigma; *st.*, style.

cases the movement is due to certain cells in the region involved becoming suddenly less turgid.

The *sleep-movements* exhibited by the leaves of some plants (cf. pp. 91, 181) can also be produced by the influence of contact. Thus, if the leaflets of the Wood Sorrel be repeatedly flicked with the finger, they will after some time show a downward movement resulting in the same position as that occupied at night (Fig. 126 N). Other kinds of Wood Sorrel which are cultivated in conservatories display these changes much more rapidly. The most striking instance is that of the familiar Sensitive Plant (*Mimosa pudica*), a member of the Pea-family. Here not only do the leaflets fold together in pairs, but with a sufficient stimulus the whole leaf even performs a downward movement. Moreover, after this has happened other adjacent leaves may undergo the same change, so that we here again have a transference of the original stimulus. In all of these

cases the organs concerned sooner or later recover their normal position, after the effect of the stimulus has passed away.

These movements, in fact all sleep-movements, are a result of changes in the degree of turgidity of the cells of the pulvinus (p. 91). Apart from the Wood Sorrel (Fig. 126) and the False Acacia already mentioned (cf. p. 91), such sleep-movements are well seen in the Dutch Clover (where the leaflets move upwards and lie face to face at night) and other members of the Pea-family (cf. Fig. 126A). The advantage of the assumption of a more or less vertical position by the leaflets at night appears to lie in the smaller surface from which radiation can take place,

FIG. 126.—Leaves of the Wood Sorrel (natural size). D, In the day-position. N, In the night-position.

so that relatively little dew is deposited in such cases. Sleep-movements of leaves are seen much more commonly in tropical plants than in our own flora.

Many flowers close at night, as for example the Tulip, the Crocus, the White Water-lily, and the Wood Anemone, and these changes are quite analogous to the sleep-movements just discussed. Similarly, the flower-heads of many members of the Dandelion-family close up at certain times, most commonly on the approach of night (*e.g.* Daisy), but in other cases at midday, as in the Salsify, whence the popular name for this plant 'John-go-to-bed-at-noon.' Night-flowering plants (*e.g.* Evening Primrose, Tobacco, cf. p. 274) have their flowers closed during

the daytime, but open them at night. In a few plants (*e.g.* Carrot) the inflorescence hangs down at night. The advantage of all these movements lies in the protection of stamens and stigma at times when the pollinating insects are not flying.

The exact external cause of sleep-movements and of these diurnal changes on the part of flowers is only imperfectly known in most cases, but since they generally follow on the daily alternation of light and darkness, associated with which is a change of temperature, these are no doubt the two influences especially concerned; in the case of the Salsify above mentioned this explanation obviously does not apply. That change of

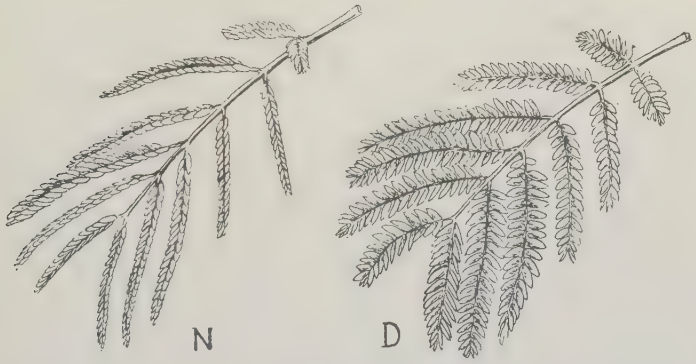


FIG. 126A.—Day- (D) and night- (N) positions of the leaflets of the bipinnate leaf of *Acacia lophantha*[1] (natural size).

temperature alone can sometimes be the determining cause of these movements is a well-known fact in the case of the Tulip, whose flowers open out widely in a warm room.

All the movements of plant-organs discussed in this and the preceding chapter take place only when other external conditions are suitable, the most important of these being an adequate temperature. At low temperatures the movements are either not exhibited at all or are performed very slowly. In the absence of the necessary amount of Oxygen for respiration they cease (cf. p. 186), and the same result is obtained if the atmosphere around the plant contains small quantities of anæsthetics

[1] This plant is very readily grown from seed and shows the day- and night-positions exceptionally well.

(*e.g.* chloroform). Unless, however, these arresting influences operate for a considerable period, their paralysing effect is only temporary. At this point we may briefly refer to the fact that, amongst the lower groups of the Vegetable Kingdom, there are green aquatic plants that swim about freely throughout the greater part of their life (with the help of minute hair-like processes from the cells, similar to those found in many microscopic animals), these movements depending, like those of higher plants, on suitable outside conditions.

In many instances an organ exhibits a curvature, even after the stimulating cause has been for some time removed, a fact which is specially obvious in the case of geotropic and heliotropic phenomena. This is readily seen if a seedling is placed horizontally for about half an hour, its lower side being marked with Indian ink, so as to be subsequently recognisable. Before any curvature of the radicle is manifest the seedling is fixed on the klinostat, so that gravity now acts equally on all sides in succession. Nevertheless, after some little time a curvature of the radicle is observed, this taking place towards the marked side. A similar result would be obtained with a plumule exposed, for the same period, to one-sided action of gravity or light, and fixed on the klinostat before a bending movement is apparent. These experiments again demonstrate that a period elapses between the reception of the impression and the occurrence of the curvature (cf. p. 209) and further that, when a stimulus has once produced an effect, this latter cannot be obliterated by subsequent exposure to uniform conditions. Similarly, if a tendril is stroked for a short time and then left untouched, a subsequent curvature nevertheless takes place.

We have thus seen that plants, in common with animals, possess a certain power of movement, though of a more limited character. All growing organs are able to bend and thus to adjust their position in relation to external influences, and in certain cases such movements are exhibited even by mature organs. Many ripe fruits (cf. Chapter XXII.) show movements of one kind or another, but these are not comparable to those just considered, since they are purely physical phenomena due to differences in the amount of shrinkage of various parts of the fruit-wall.

CHAPTER XVIII

The Inflorescence and the General Structure of the Flower

We have so far almost confined our attention to the vegetative organs [1] of the plant, but we have still to consider the culmination of the plant's activities in the formation of flowers and seeds. In this way, as the Shepherd's-purse has shown us (p. 7), plants not only reproduce their kind, but also multiply the number of individuals. We have noticed that this may also be achieved by vegetative propagation (cf. Chapter XII.) in which portions of the vegetative body get detached and give rise to new plants. Reproduction by seeds, however, has greater advantages than vegetative multiplication, owing to the fact that seeds are usually capable of being carried to a considerable distance from the parent, so that there is no competition between it and its offspring (cf. p. 165).

In the first place we may deal with the way in which the flowers are arranged, *i.e.* with the *inflorescence.* In the simplest case the flowers are borne singly (*i.e.* they are *solitary*), either terminally as in the Crocus (Fig. 90 A), Tulip, Wood Anemone, Winter Aconite (Fig. 142), etc., or in an axillary position as in the Yellow Pimpernel. As a general rule, however, they are arranged to form an inflorescence which in essentials exhibits two types of branching, similar to those found in the vegetative part of the shoot, viz. monopodial and sympodial (Chapter VII.); but the same terms are not usually employed, a monopodially branched inflorescence being described as racemose, and a sympodially branched one as cymose.

Each flower of such inflorescences usually arises in the axil of a leaf (*bract,* Fig. 127, *br.*) which is often considerably modified

[1] These consist of root, stem, and leaves, *i.e.* of the plant apart from its flowers.

and in most cases serves essentially as an organ for the protection of the flower-buds. In many plants the bracts are far simpler in form than the foliage-leaves (*e.g.* Monkshood) and are indeed often little more than scale-leaves devoid of chlorophyll (*e.g.* Hyacinth); occasionally bracts are altogether absent (Wall-flower and other members of the Cruciferæ [1]). The term bract is also applied to the large sheathing leaves enveloping the inflorescence of some forms (*e.g.* in the Narcissus and Cuckoo-pint, Fig. 158 A), although such structures are also spoken of as *spathes*. The flower-stalk (or *peduncle*) itself frequently bears one or more small leaves which are often scaly and are known as *bracteoles* (Violet, Hyacinth, etc.). In the Wood Anemone the peduncle, a little way beneath the flower, bears a whorl of three palmately lobed bracteoles which are but slightly modified from foliage-leaves (see also Fig. 142). Attention should be drawn to the fact that the terms bract and bracteole are purely topographical, the structures concerned, though always leafy, being very diverse both as to form and function.

The most characteristic feature of a *racemose inflorescence* is that it usually possesses a prominent main axis which generally continues to grow and produce lateral flowers for some time; also these invariably *open from below upwards*, so that the oldest are at the base and the youngest at the apex. The simplest type is the *raceme* (Fig. 127 A) in which the lateral branches of the main axis each bear a single flower (*e.g.* Currant, Lupine, Germander Speedwell, Bird's-nest Orchid, Fig. 77); in some cases the main axis itself ultimately terminates in a flower (*e.g.* Monkshood, Hyacinth), whilst in the Foxglove and Tooth-wort (Frontispiece), for instance, all the flowers of the raceme are twisted over to one side. In those cases in which the lateral branches themselves bear racemes of flowers (Fig. 127 D) we speak of a *compound raceme*, good instances being furnished by Oats, Fescue, and other Grasses.

A slight modification of the raceme, tending to make the group of flowers more conspicuous, is that known as the *corymb* (Fig. 127 B, Fig. 146*). Here the lower peduncles become increasingly longer, so that all the flowers lie on the same level, a condition well illustrated by the Candytuft and many other

[1] The distinctive features of this and other natural orders to be mentioned in the subsequent chapters are summarised in Chapter XXIII.

Cruciferæ (*e.g.* Shepherd's-purse, Fig 1); in this family, however, the uniform level is lost in the fruiting stage through elongation of the internodes between the individual fruits (cf. Fig. 1).

Similar conspicuity is attained by the *umbel* (Fig. 127 C) in which all the peduncles arise from the apex of the flower-bearing stem, the bracts of the individual flowers forming a whorl

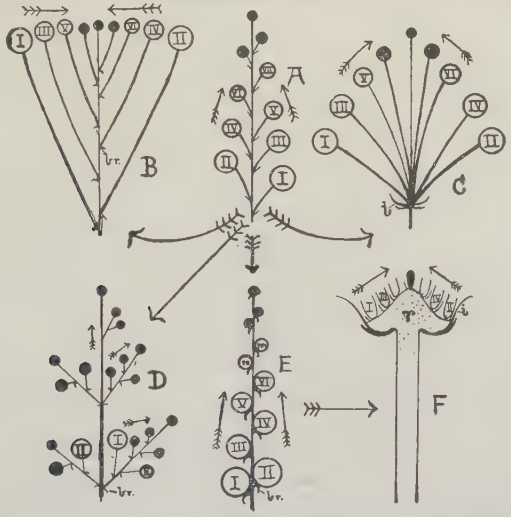


FIG. 127.—Diagrams of different types of racemose inflorescences. A, Simple raceme. B, Corymb. C, Simple umbel. D, Compound raceme. E, Spike. F, Capitulum. The Roman numerals, as well as the small arrows, indicate the order of opening of the flowers. The larger arrows show the relation of the different types to one another. *br.*, bracts; *i*, involucre; *r*, receptacle.

(the *involucre, i*) at this point; examples are furnished by the White Clover (Fig. 149 A), Cherry, and Cowslip, whilst the Primrose has an umbel in which the separate peduncles arise from amidst the radical leaves. We can regard the umbel as a raceme in which the flower-bearing portion of the main axis has been much shortened, but here, as in the corymb, the racemose character is clearly indicated by the order of opening of the flowers, viz. from without inwards. As in the compound raceme, the single flowers of the umbel may be replaced by branches

bearing secondary umbels, and such *compound umbels* are far commoner than the simple ones and specially characteristic of the Umbelliferæ (*e.g.* Hogweed, Carrot). In such inflorescences we frequently find a whorl of bracts, not only at the first point of branching, but also at the base of each secondary umbel, although one or other of these whorls is often absent.

Returning to the simple raceme, another modification results from the individual flowers being sessile (*i.e.* without a peduncle), in which case we speak of the inflorescence as a *spike* (Fig. 127 E) ; good examples are seen in the Black Plantain or Ribwort (Fig. 128), the Pondweeds (Fig. 139*, *In.*), and

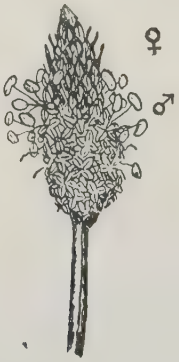


Fig. 128.—Spike of the Black Plantain or Ribwort (natural size). The upper flowers (*i.e.* those which have opened most recently) are in the female (♀) stage, whilst the middle ones are now in the male (♂) stage and the lowest of all are already fading (cf. p. 252).

the Vervain. The *catkins* of the Willow, Poplar, and Hazel (Fig. 129, ♂) are a form of loose spike with relatively conspicuous bracts and flowers which contain either stamens or ovary only.

If the axis of a spike be telescoped down, with a consequent expansion in width, we obtain the so-called *capitulum* (Fig. 127 F., Fig. 145 A), particularly characteristic of the Compositæ (*e.g.* Daisy, Hawkweed, etc.). The minute flowers (florets) in such an inflorescence are densely crowded together on a convex receptacle (Fig. 127 F, *r*) which can be recognised as a condensed axis in forms like the Daisy and Chamomile, since

here, towards the end of flowering, it becomes elongated and conical. Surrounding the capitulum are numerous greenish bracts, together constituting the *involucre* (*i*), those belonging to the individual florets being represented by small scales in the Sunflower and Cat's-ear, although usually absent. It is again the outermost flowers of the capitulum that open first.

The great characteristic of *cymose inflorescences* is that the growth of any given axis terminates at an early stage with the production of a flower which opens before those on the lateral branches arising below it; hence the order of opening is *from above downwards*. Good examples of *simple cymes* (Fig. 130 A) are afforded by the Buttercup, Herb Bennett (Avens), and the Poppy (Fig. 116). In all such cases the further growth of the

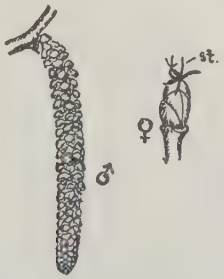


FIG. 129.—Male (♂) and female (♀) catkins of the Hazel (natural size). *st.*, stigmas.

inflorescence is carried on from the axil or axils of bracteoles of the terminal flower, which thus become the bracts of the lateral flowers (Fig. 130 A). Where the bracteoles are opposite, as for instance in the Caryophyllaceæ (*e.g.* Stitchwort, Campion) and the Centauries, the lateral branches are opposite (Fig. 130 B). As a result, an apparent forking of the axis of the inflorescence takes place, as in the case of dichasial branching of the stem (p. 78), so that we can speak of a *dichasial cyme*. Frequently, however, as in the Mouse-ear Chickweed, one of the two branches is shorter than the other and, in the later branchings, altogether fails to develop.

One occasionally finds cymose inflorescences closely resembling some of those of the racemose type. For instance, the Garlic and Onion have cymose umbels, whilst in the Scabious

we have a cymose capitulum, and in the Wayfaring Tree a cymose corymb. In all such cases, however, the nature of the inflorescence can be recognised by the order of opening of the flowers which, in these cymose types, do not develop in regular sequence from without inwards.

In richly branched inflorescences we not infrequently get a combination of both types, the primary arrangement being generally racemose, whilst the later branchings are cymose. Thus, in the Lilac and Horse Chestnut the flowers as a whole open from below upwards, but on each branch the terminal one is the first to expand. In the Labiatæ (*e.g.* Calamint, Ground Ivy, Fig. 8, Dead-nettle, etc.), as well as in the Purple Loosestrife,

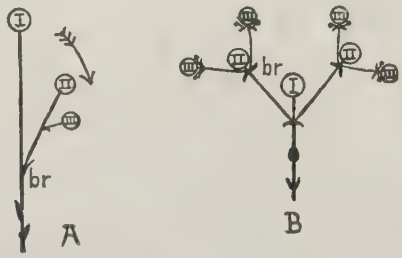


FIG. 130.—Diagrams of cymose inflorescences. A, Simple cyme. B, Dichasial cyme. The Roman numerals and the arrow in A indicate the order of opening of the flowers. *br.*, bracts.

the axillary groups of flowers develop from below upwards (*i.e.* are racemose), whilst each group is a dichasial cyme.

The individual flower [1] may be regarded as a compressed shoot, serving for purposes of reproduction and bearing a number of different structures which are usually not separated by internodes. Of these floral organs some are essential for the production of seed (viz. stamens and ovary), whilst others constitute the non-essential *perianth* (viz. the calyx and corolla of the Shepherd's-purse, Fig. 4) which, however, mostly plays an important part in the protection of the flower and in the attraction of insect-visitors. When the flower, as in the Ash, contains only the essential organs it is said to be *naked* (Fig. 139*).

The expanded end of the peduncle to which the different

[1] The reader is advised to study once more the flower of the Shepherd's-purse (p. 6) before passing on to the subsequent matter.

floral organs are attached is spoken of as the *receptacle* or *thalamus*. This is frequently more or less convex in form, bearing at its summit the ovary, with stamens and perianth (or corolla and calyx) at successively lower levels (Fig. 131 A). Such flowers are well illustrated by the Buttercup (Fig. 132 A) and Tulip, and are said to be *hypogynous*. Occasionally the receptacle is flattened, the ovary occupying the centre, whilst the other floral organs arise from its edge; such a flower is still hypogynous, a good instance being the Sycamore. In some Spiræas (Fig. 131 B) the receptacle is likewise flat, but the ovary is borne on a central

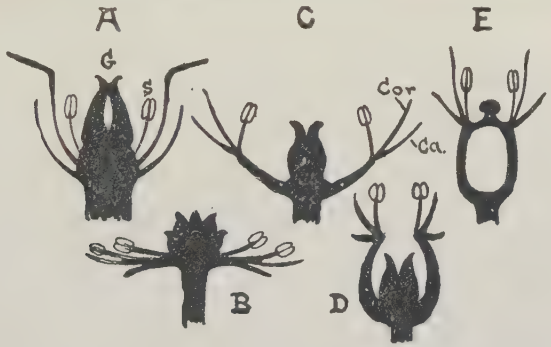


FIG. 131.—Diagrams to show different types of floral receptacle. A, Hypogynous flower. B, Flower with flat thalamus. C, Perigynous flower. D, Extreme perigynous type. E, Epigynous flower. Receptacle and ovary shown in black in all cases. *Ca.*, calyx; *Cor.*, corolla; *G*, ovary; *S*, stamen.

protuberance. From a flattened receptacle it is but a slight step to one which is more or less deeply concave (Fig. 131 C and D); examples are furnished by the Strawberry, the Agrimony, and the Rose (Fig. 131 D), these three forms showing progressive hollowing out of the thalamus, so that the central ovary (which in the first and last instances is situated on a central protuberance) becomes more and more enclosed. Such flowers are described as *perigynous*. If the ovary becomes completely enveloped and altogether joined up with the receptacle (Fig. 131 E), whilst the remaining floral organs arise from its top, we obtain an *epigynous* flower, such as is found in the Umbelliferæ (*e.g.* Hogweed, Fig. 146 E) and the Narcissus (Fig. 132 B). It is obvious that, in

such a flower the ovary is situated below the other organs and is therefore said to be *inferior*, whilst in peri- and hypogynous flowers it is described as *superior*.

In certain hypogynous flowers (*e.g.* the Mouse-tail, Celery-leaved Buttercup) the receptacle is markedly elongated and in such cases the different organs are generally arranged spirally. Most flowers, however, have their various organs grouped in

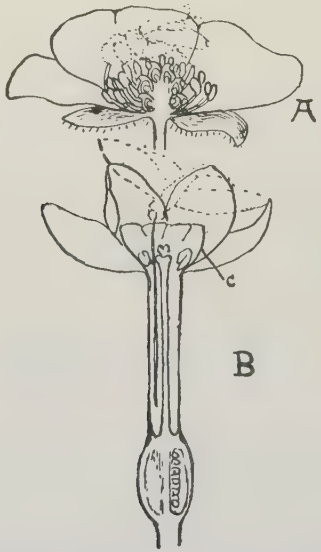


FIG. 132.—Vertical sections of flowers of A, Buttercup (open type); B, Pheasant's-eye Narcissus (tubular type), showing hypogyny and epigyny respectively. The body of the pollinating insect is shown by dotted lines, the proboscis being indicated by a continuous line. *c*, corona.

whorls which in rare cases are even separated by marked internodes; thus, in the Bladder Campion such an internode occurs between calyx and corolla, whilst in the Passion-flower there is one between corolla and stamens.

The features hitherto considered are best illustrated by means of *longitudinal sections* through the middle of the flower, as in Fig. 131. In drawing such sections it is advisable to show only the actual cut surface (cf. Fig. 133 B), which is easily done

after a little practice, even by those who possess but slight skill in drawing. Such a section should faithfully represent the shape of the receptacle, as well as the order of attachment of the floral organs, and should indicate, as far as possible, the position of bracts and bracteoles with reference to the flower.

Apart from the longitudinal section, a *floral diagram* or ground-plan of the flower is necessary to make its structure quite plain. For this purpose (cf. Fig. 133 A) the main axis (*m.a.*), on which the flower is borne, is shown by a dot and after that the exact position of the different floral whorls, as well as of the bracts and bracteoles, with reference to the main axis and to one another, is indicated (as in Fig. 133 A and C–F); all the members arising at one level are placed on the same circle and the ovary is shown in cross-section. The side of the flower adjacent to the axis of inflorescence is called the *posterior* side, whilst that away from the axis is termed the *anterior* side. A longitudinal section which passes from the posterior to the anterior side of the flower is said to be cut through the *median plane* and is the customary direction in which such sections are made.

The floral diagram of the Hyacinth (Fig. 133 A) shows that all the different whorls have their parts in threes; this is characteristic of Monocotyledons and such a flower is said to be *trimerous*. On the other hand, the Geranium (Fig. 133 E), a Dicotyledon, has its parts in fives and its flower is consequently described as *pentamerous*, a type of frequent occurrence in the latter group, although flowers with their parts in fours (*i.e.* *tetramerous*, as in the Willow-herb, Fig. 144), or twos (*e.g.* Enchanter's Nightshade), are also found.

From the diagrams in Fig. 133 it will be seen that the ordinary flower, both in Monocotyledons and Dicotyledons, has two whorls of perianth-members. In Monocotyledons (Fig. 133 A) the main axis lies opposite the interval between two members of the outer whorl—that is to say, the third member is anterior, whereas in most Dicotyledons the odd (fifth) member of the outer perianth-whorl is situated opposite the axis,—in other words is posterior (Fig. 133 D and E). The Leguminosæ (*e.g.* Sweet-pea, Fig. 133 C) are exceptional in this respect, the odd sepal here being anterior. It will be noticed that in general the members of one whorl alternate with those of the next

and, although this is without exception in the case of the perianth, it is not uncommon in Dicotyledons for the outer whorl of stamens to stand opposite the petals (*e.g.* Geranium, Fig. 133 E). The number of whorls, moreover, varies in the flowers of different plants ; apart from the absence of a perianth

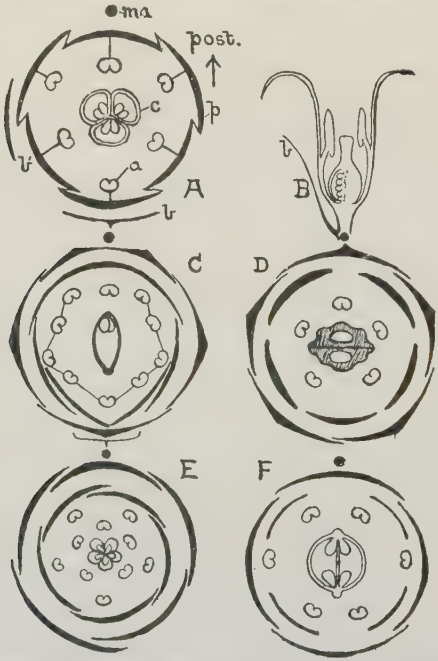


FIG. 133.—Diagrams of floral structure. A and C–F, Floral diagrams. A, Hyacinth (Liliaceæ). C, Sweet-pea (Leguminosæ). D, Hogweed (Umbelliferæ). E, Geranium. F, Wallflower (Cruciferæ). *a*, stamen ; *b*, bract ; b^1, bracteole ; *c*, ovary ; *m.a.*, main axis ; *p*, perianth-member ; *post.*, posterior side of flower. B, Longitudinal section of flower of Hyacinth, taken through the median plane. *b*, bract.

(*e.g.* Ash, see above), there may be only one whorl of stamens (*e.g.* Umbelliferæ, Fig. 133 D) or more than two (*e.g.* Rosaceæ). In the Tulip (Fig. 133 A) and Geranium (Fig. 133 E) the same number of parts occurs in each whorl, but this is by no means the general rule, the ovary frequently consisting of less (two in Umbelliferæ, Fig. 133 D ; one in Leguminosæ, Fig. 133 C),

and not uncommonly this is true also of the stamens (*e.g.* the Speedwell, with a tetramerous perianth and two stamens, Fig. 174 B).

We may next proceed to consider the *non-essential organs* of the flower. The two alternating whorls are, in the case of Monocotyledons, usually alike in colour and texture, so that the collective term perianth can alone be employed. In Dicotyledons, on the other hand, as well as in some Monocotyledons (*e.g.* Water Plantain, Arrowhead), the outer whorl is generally green and protective, whilst the inner one is brightly coloured and attractive, and we then speak of a *calyx* and *corolla* respectively. Occasionally there is only one perianth-whorl, which is then generally green, and good examples of such *apetalous* flowers are furnished by the Stinging Nettle and Dog's Mercury (Fig. 134).

Fig. 134.—Apetalous, unisexual flowers of the Dog's Mercury (somewhat enlarged). The left-hand one is the male, the right-hand one the female.

The individual members of the calyx are spoken of as *sepals* and with rare exceptions are green in colour. Their protective character is well seen in most flower-buds in which all the inner parts are completely enveloped by the sepals, which either fit edge to edge (*i.e.* are *valvate*, as in the Old Man's Beard) or more commonly overlap (*i.e.* are *imbricate*, as in the Buttercup; cf. also Fig. 133 C–E). In some cases (*e.g.* the Poppy, Fig. 116, *c*) the sepals actually drop off as the flower expands and the necessity for protection becomes less urgent. As a general rule, however, the calyx is *persistent* and may subsequently, long after the petals and stamens have withered, afford protection to the fruit (*e.g.* Campion, Mallow, Fig. 160 C) or even aid in its dispersal (cf. p. 286).

The necessity of the calyx as a protective envelope is easily demonstrated by carefully removing it from a number of young buds (Poppy and Rose answer well) without damaging

the rest of the flower ; as a result the latter will be found either to dry up or to show half-withered petals when it expands.

The sepals are usually simple in form and either arise quite separately from one another (*i.e.* are *polysepalous*, as in the Geranium, Fig. 133 E, and Wallflower, Fig. 147) or are more or less completely joined to form a tube with free tips corresponding to the component members (*i.e.* are *gamosepalous*, as in Fig. 135 B and C, shown by joining edges of sepals in floral diagram). When the individual lobes of a gamosepalous calyx are of the

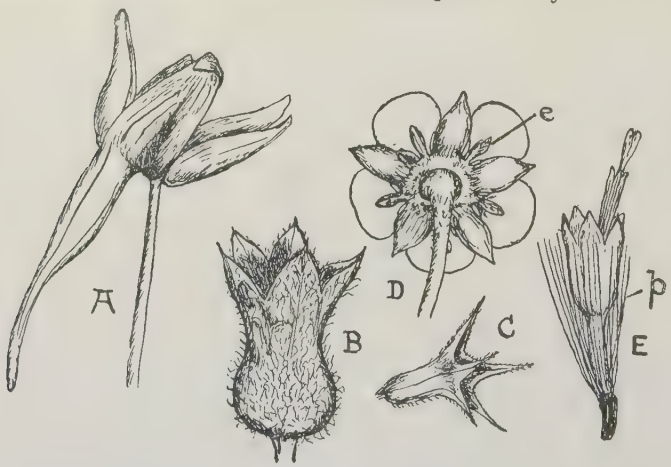


FIG. 135.—Forms of calyx (A–D natural size, E enlarged). A, Garden Nasturtium (spurred). B, Henbane (gamosepalous). C, Dead-nettle (gamosepalous and slightly irregular). D, Herb Bennett. *e*, epicalyx. E, Tubular floret of Aster (Compositæ). *p*, pappus

same size it is said to be *regular* (Henbane, Fig. 135 B), but frequently owing to unequal development an *irregular* calyx is produced (*e.g.* the two-lipped calyx of many Leguminosæ, Fig. 150 A and B) ; less commonly a polysepalous calyx shows irregularity, as in the Garden Nasturtium (Fig. 135 A) in which one side is produced into a long tube (*spur*). Where the flowers are closely massed together in the bud, so that they afford one another mutual protection, the calyx is often greatly reduced. Thus, in the Umbelliferæ it merely forms a green rim, whilst in the capitula of Compositæ, in which additional protection is afforded by the involucre, the leaf-like character of the sepals

is altogether lost, the calyx generally consisting of a circle of hairs (the *pappus*, Fig. 135 E, *p*) developed to aid in fruit-dispersal (cf. p. 286).

The *petals* of the corolla in Dicotyledons and of the perianth in Monocotyledons exhibit a great variety of form, developing either separately (*polypetalous*, as in the Buttercup, Fig. 132 A, Water Plantain, and Tulip) or being more or less joined together so as to form a corolla-tube with free lobes (*gamopetalous*, as in the Primrose, Fig. 148, Harebell, Fig. 137 A, and Narcissus, Fig. 132 B). Free petals are usually much larger than the sepals and very commonly have an entire margin (*e.g.* Buttercup, Fig. 132 A, Herb Bennett, Fig. 136 B), although sometimes more or less deeply divided (*e.g.* Campion, Fig. 168 A, Stitchwort, Fig. 168 B, Ragged Robin). As a general rule the petal

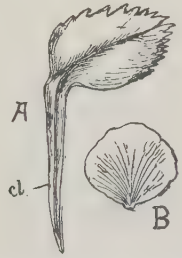


Fig. 136.—Forms of petals (about two-thirds natural size). A, Pink. B, Herb Bennett. *cl*, claw.

has only an extremely short stalk (Fig. 136 B), but occasionally (*e.g.* Pink, Fig. 136 A, Wallflower) the blade terminates a long claw (*cl.*) with which it forms almost a right angle.

The gamopetalous corolla shows considerable diversity of form, being either bell-shaped (Harebell, Fig. 137 A, Hyacinth), urn-shaped (Cross-leaved Heath, Fig. 137 B, Grape Hyacinth), funnel-shaped (Convolvulus, Fig. 137 C), or *tubular* (*e.g.* the Comfrey and the inner florets of the capitula of many Compositæ, Fig. 135 E). As in the case of the calyx, the corolla may be *regular* (*e.g.* all the instances just quoted) or *irregular*; examples of the latter condition are furnished by the *bilabiate* corolla of the Dead-nettle (Fig. 137 D) and many other Labiatæ, and by the *personate* corolla of the Snapdragon (Fig. 153), in which the opening to the tube is completely closed owing to the peculiar shape

of the petals. An irregular corolla may, however, also occur amongst polypetalous forms, as for example the butterfly-shaped (*papilionaceous*) corolla of the British Leguminosæ (Fig. 150) and that of Orchids (Fig. 156).

Since the space within the flower-bud is as limited as in a vegetative bud, the developing petals become folded just as do the young foliage-leaves (cf. p. 98). Most commonly the petals overlap one another, so that their arrangement is *imbricate* (Fig. 133 C and E); more rarely we get a crumpled folding

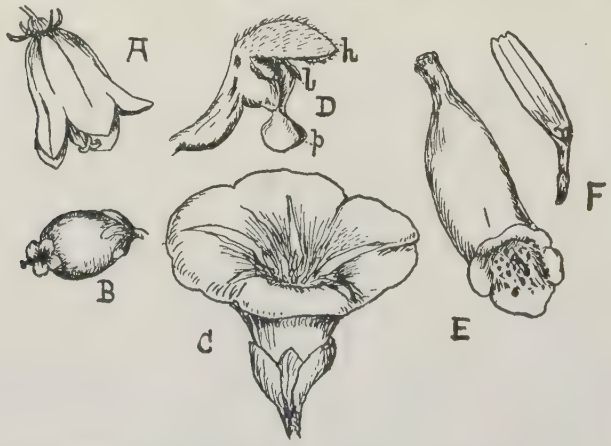


FIG. 137.—Forms of gamopetalous corolla (all natural size). A, Harebell (bell-shaped). B, Cross-leaved Heath (urn-shaped). C, Convolvulus (funnel-shaped). D, Dead-nettle (bilabiate). *h*, upper lip (hood); *l*, side-projections; *p*, lower lip (alighting platform). E, Foxglove. F, Ray-floret of Compositæ (strap-shaped).

(as in the Poppy, Fig. 116, *b*, and Rock-rose) or a twisted arrangement (as in the Gentians, Fig. 138 A and C, and Mallows).

In the same way as outgrowths, such as stipules and the ligule of Grasses (p. 91), have been found arising at different points from foliage-leaves, so also analogous structures occasionally develop in relation to the calyx and corolla. Thus, in some plants leafy processes develop between the bases of adjacent sepals, so that there appear to be two alternating whorls of the latter, the outer of which is then spoken of as an *epicalyx* (*e.g.* Strawberry; Herb Bennett, Fig. 135 D, *e*; Mallow). Similarly

tubular corollas may produce outgrowths, usually near the top of the tube, which either arise independently from each petal (*e.g.* the teeth-like processes of the Campion, Fig. 168 A), or form

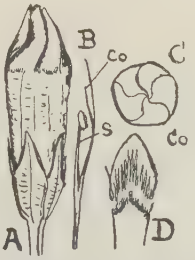


FIG. 138.—Structure of flower of Gentian (natural size). A, Entire flower-bud, showing twisted arrangement of petals. B, Longitudinal section of petal, showing epipetalous stamen and corona. C, Petals in bud, seen from above. D, Single petal, showing corona. *co*, corona ; *s*, stamen.

a united fringe (as in the Gentian, Fig. 138 B and D, *co.*), or a complete membranous tube (the *corona* of Daffodil and Narcissus, Fig. 132 B, *c*).

CHAPTER XIX

The Essential Organs of the Flower

Of the essential organs of the flower the *stamens* always lie outermost and may therefore be considered next. Each

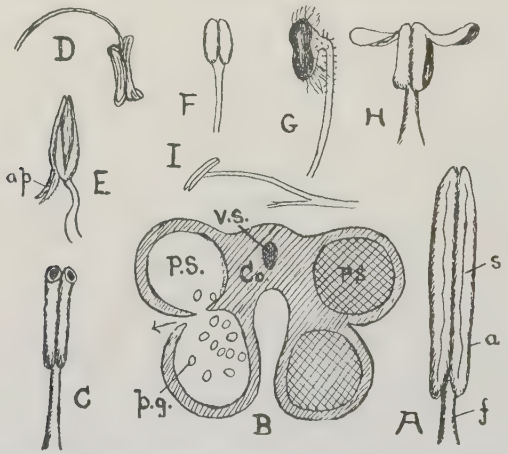


Fig 139.—Stamens and stamen-structure (all natural size except B, which is enlarged about 10 times). A, Tulip. *a*, anther; *f*, filament; *s*, line of dehiscence in right-hand anther-lobe. B, Cross-section of stamen of same. *Co.*, connective; *p.g.*, pollen grain; *P.S.*, pollen sacs; *V.S.*, vascular strand of connective. The right-hand part shows the young, the left-hand part the mature anther. The arrow shows the line of dehiscence. C, Rhododendron, showing dehiscence. D, Vernal Grass. E, Heather or Ling, showing dehiscence. *ap*, appendages. F, Buttercup. G, Dead-nettle. H, Bay Tree (*Laurus*), showing dehiscence. I, Honeysuckle, showing epipetaly (represented in floral diagram as in Fig. 133 A).

stamen consists of a stalk or filament (Fig. 139 A, *f*) and a swollen pollen-producing part or anther (Fig. 139 A, *a*). Most

commonly the anther is rigidly attached to the filament (as in Fig. 139 A, C, F and H), but occasionally (as in Grasses, Fig. 139 D, and the Honeysuckle, Fig. 139 I) it is more or less loosely suspended from its end.

If we cut a cross-section of the anther of a young stamen (*e.g.* of the Tulip, Fig. 139 B), examination with a lens will show two pairs of cavities or *pollen-sacs* (*P.S.*), one pair situated in each of the two lobes of the anther and traversing their full length; the two anther-lobes are joined together by a middle piece or *connective* (*Co.*) in which a small vascular strand (*V.S.*) is distinguishable. In a more mature anther the *pollen grains* (*p.g.*) can be recognised as a powdery mass within each pollen-sac, and at this stage the partition separating the two sacs in each lobe has generally broken down, so that they form one continuous cavity (Fig. 139 B, left-hand portion). This opens to the exterior by a slit extending the whole length of the anther-lobe (Fig. 139 A, *s*; shown by the arrow in Fig. 139 B), the two flaps on either side of the slit curling back in dry air, so as to leave a wide opening from which the pollen is readily removed.

The structure just described is typical of nearly all stamens, the most important differences lying in the method of opening or *dehiscence*. This, in the vast majority of cases, takes place by means of longitudinal slits as in the Tulip, such dehiscence being due to a withdrawal of moisture from the surface-layers of the anther-wall; it is this which leads to the wide curling back of the flaps on either side of the slit when the air is dry. In damp weather, on the other hand, the flaps often bend forwards again, so as to more or less close the opening and protect the pollen. According as the connective faces outwards or inwards the dehiscence of the anthers takes place towards (viz. *introrsely*, *e.g.* Umbelliferæ, Fig. 133 D), or away from, the centre of the flower (*i.e. extrorsely*, *e.g.* Buttercup, Fig. 167, Iris, Convolvulus), a feature which is generally related to the position of the honey. Other methods of dehiscence are exemplified by the Heather (Fig. 139 E), in which the slit is confined to the upper part of each anther-lobe, by the Potato and Rhododendron (Fig. 139 C), where the pollen is shaken out of a pore at the top of each lobe, and by the Bay Tree (Fig. 139 H), in which the anther opens by a pair of valves.

Occasionally appendages develop on the anthers (as in the Heather, Fig. 139 E, *ap.*) or, in rare instances, the connective branches, so that the two anther-lobes are more or less widely separated (*e.g.* Hornbeam, Sage, Fig. 152 E). In the Violet (Fig. 155 B, *c*) and Herb Paris the connective forms a membranous prolongation beyond the anther, an extreme condition of which is seen in the Pondweeds, where the expanded connectives (Fig. 139*, *co.*) of the four stamens closely resemble a perianth.

As a rule, if more than one whorl of stamens is present, the individual whorls alternate with one another (Fig. 133 A and E). When but a single one occurs (*e.g.* Umbelliferæ, Fig. 133 D), as well as when several whorls are represented (Fig. 133 A),

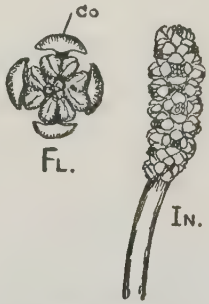


Fig. 139*.—Flower (*Fl.*) and inflorescence (*In.*) of the Floating Pondweed (the flower enlarged, inflorescence natural size). *co.*, connective.

the outermost stamens not uncommonly alternate with the inner series of perianth-leaves, but we have already noticed (p. 234) that this is not without exception. Thus, in the Primrose (Fig. 172) the five stamens are situated opposite the petals, whilst in the Geranium (Fig. 133 E) the outermost whorl occupies the same position. When the stamens are numerous, their number is usually subject to considerable variation and we speak of them as *indefinite*; such indefinite stamens are not uncommonly spirally arranged, as in the Buttercup (Fig. 167) and Marsh Marigold. In general all the stamens are of the same length, but in the Cruciferæ (*e.g.* Wallflower) there are four long and two short (*tetradynamous*), and in many members of the Labiatæ two long and two short ones (*didynamous*), whilst in the Stitchwort five of them are longer than the other five (Fig. 168 B).

The number of stamens is often equal to, or some multiple of, the number of members in the perianth-whorls (Fig. 133 A and C–E), but there are frequent exceptions to this. Instances are most usually found in flowers having only a single whorl of stamens and possessed of an irregular corolla, *e.g.* in the Labiatæ (Fig. 173) and Scrophulariaceæ (Fig. 174 C), in both of whichthere are generally only four stamens ; other examples are furnished by the Speedwell (Fig. 174 B) and Rosemary with only two, and the Garden Nasturtium with eight stamens. In these cases a careful study of the arrangement of those stamens which are present shows that one or more have failed to develop, and confirmation is furnished by flowers in which a sterile structure

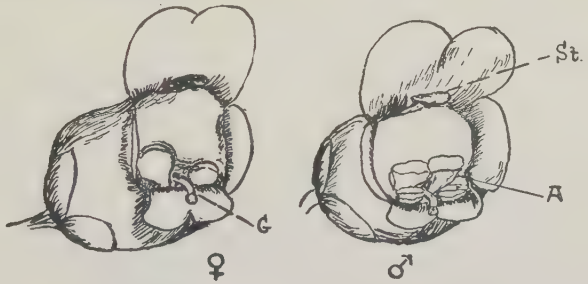


FIG. 140.—Flowers of the Figwort, to illustrate protogyny (enlarged). The left-hand flower is in the female stage, whilst in the right-hand one the stigma has withered and the stamens are mature. *A*, stamen ; *G*, stigma ; *St.*, staminode.

or *staminode*[1] (not producing pollen) occupies the position of the missing stamen. This is well illustrated by the Figwort, a member of the Scrophulariaceæ, in which the staminode appears as a small reddish-brown projection (Fig. 140, *St.*) occupying the posterior position in the stamen-whorl (Fig. 174 C) which, in most other members of this family and of Labiatæ, is left vacant. Other examples of such staminodes are found in Pentstemon and the Stork's Bill, the latter having a complete whorl of five staminodes situated opposite the petals.

As in the case of calyx and corolla, the stamens may either be free from one another or joined together in various ways.

[1] In the floral diagram this is indicated by a small circle or in the way shown in Fig. 174 C ; missing stamens are marked by a dot (cf. Fig. 174 B).

Thus, in the Needle Furze (Fig. 170), Broom, and Gorse the ten filaments are united for the greater part of their length (*i.e.* are *monadelphous*), so as to form a tube round the young pod. A somewhat similar condition is seen in the Mallow and Hollyhock, where the numerous stamens have joined filaments. In the Compositæ (Fig. 145) and the Sheep's-bit, on the other hand, the five filaments are free, whereas the anthers are connected (*i.e.* are *syngenesious*). Moreover, in many flowers with tubular corollas the filaments of the stamens are more or less completely fused with the petals, a condition described as *epipetalous* (Figs. 133 B, 138 B and 139 I); in this case they appear to arise from the petals themselves. Finally it may be noticed that in a few flowers the stamens exhibit branching, those of the St. John's Wort for instance, forming five bundles each dividing into numerous filaments bearing anthers.

The *ovary* is composed of one or more structures known as *carpels* which may either be joined together to form a *syncarpous* ovary (*e.g.* Liliaceæ, Fig. 133 A, *c*) or free from one another, when the ovary is said to be *apocarpous* (Buttercup, Fig. 132 A, Fig. 141 C). The nature of the carpels is best seen in ovaries of the latter type. Thus, in a young fruiting specimen of the Larkspur or Monkshood (Fig. 159, *b*) one edge of each carpel bears a prominent midrib (or *dorsal suture*, *m*), from which lateral veins (*l.v.*) are seen to arise; on the opposite edge there is a slight furrow, and it is along this line (the *ventral suture*) that the young seeds are attached on the inner face of the fruit and that the latter subsequently opens. Similarly, if a young pod of a Pea be split lengthwise, it will be found to break more readily along the edge bearing the young seeds (*i.e.* the ventral suture); moreover, the latter are seen to occur on both valves, since some remain attached to one half and some to the other. In the Dyer's Weed the margins of the carpels are not joined together, except at the base, even in the young ovary. All the Conifers (cf. p. 351) have flat carpels bearing the ovules freely exposed on their upper surface.

The examples given illustrate the fact that the carpels are to be regarded as leaf-like structures in which the dorsal suture constitutes the midrib. In an apocarpous ovary the carpels are folded so that their margins meet, each edge usually bearing a number of seed-rudiments or *ovules* (Fig. 141 D) and being

generally somewhat swollen to form the *placenta*. The tip of each carpel is produced into a slender outgrowth, the *style*, which terminates in the *stigma*.

In the syncarpous ovary the sides of adjacent carpels are more or less joined together, and a first step in this direction is seen in the Monkshood (Fig. 159, *b*) and Larkspur in which the individual carpels are frequently united at their bases by the ventral sutures. When the carpels are completely connected in this way, we obtain an ovary divided by partitions or *septa* into as many compartments or *loculi* as there are carpels, the structure being described as *bi-*, *tri-*, *quadri-*, or *multilocular*

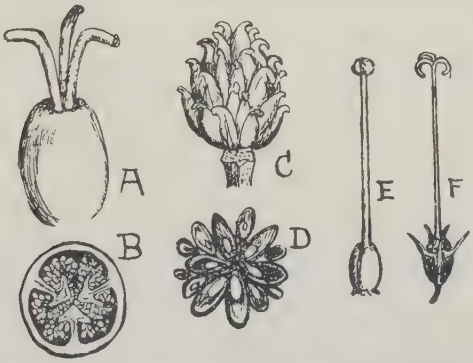


FIG. 141.—Ovaries and ovary-structure (E and F natural size, the other figures enlarged). A, Ovary of St. John's Wort. B, The same in cross-section. C, Ovary of Buttercup. D, The same in cross-section. E, Ovary of Foxglove. F, Ovary of Canterbury Bell.

according to their number; thus, the Umbelliferæ (Fig. 133 D) and the Scrophulariaceæ (*e.g.* Snapdragon, Fig. 153 D) have a bilocular, the Hyacinth (Fig. 133 A) has a trilocular, the Willow-herb has a quadrilocular, and the Love-in-a-Mist a multilocular ovary. If only one carpel is present we have a *monocarpellary* ovary, as in Leguminosæ (Fig. 133 C).

A second mode of junction of the carpels in syncarpous ovaries is that in which adjacent edges are united without the individual carpels being folded together, the ovary consequently having only one compartment (*i.e.* it is *unilocular*, *e.g.* Violet, Fig. 155 C, St. John's Wort). The ovary is then described as *bi-*, *tri-*, *quadri-*, or *multicarpellary* according to the number of

component carpels, and this feature can be determined either by the character of the style and stigma or by the arrangement of the ovules (see next two paragraphs).

Whatever the type of syncarpous ovary, the tips of the individual carpels are either free or more or less joined. Thus, in some ovaries the styles and stigmas are quite distinct (*e.g.* the St. John's Wort, Fig. 141 A) and in such a case the number of component carpels is quite apparent. More usually, however, the styles of a syncarpous ovary are completely united to form a single structure, the stigma dividing into as many segments as there are carpels, *e.g.* five in Crane's Bill, Fig. 160 B; four in the Rose-bay Willow-herb, Fig. 144; three in the Canterbury Bell, Fig. 141 F; two in Compositæ, Fig. 137 F, and in the Foxglove, Fig. 141 E. The examples show that the stigma either divides into a number of narrow arms or is merely lobed, and in most cases the actual sticky receptive surface (on which the pollen can alone germinate) is situated on the upper side. In the ovary of the Primrose (Fig. 148), however, neither style nor stigma are divided, the latter merely constituting a small swelling (a so-called *capitate* stigma) at the end of the former. The almost flat top of the multicarpellary ovary of the Poppy (Fig. 159, *h*) bears a number of dark radiating lines which represent stigmas of a peculiar type, the style being altogether absent in this case.

In each compartment of a syncarpous ovary of the first type above described the ovules are naturally situated on the central column (placenta), formed by the fused and somewhat swollen margins of the carpels (Figs. 132 B, 133 B); the arrangement or *placentation* of the ovules in this case is said to be *axile* (*e.g.* Hyacinth, Fig. 133 A, Snapdragon, Fig. 153 D). On the other hand, when the carpels are joined together by their edges and the ovary is unilocular, the ovules are borne in rows (frequently two) along the lines of junction, so that we can speak of marginal or *parietal* placentation (*e.g.* Violet, Fig. 155 C). Where this is found, the number of placentas again gives an indication of the number of carpels composing the ovary. In some plants the parietal placentas project more or less markedly into the cavity of the ovary, as for instance in the St. John's Wort (Fig. 141 B) and the Poppy. A third type of placentation is seen in the Caryophyllaceæ (*e.g.* Campion) and Primulaceæ

(*e.g.* Primrose, Fig. 148) in which the ovules are borne on a central upgrowth arising from the base of the ovary, a so-called *free central placenta*; in the former family septa are occasionally found connecting the placenta with the ovary-wall. A peculiar kind of placentation (*superficial*) is seen in the White Water-lily and in the Flowering Rush, in which the ovules arise from the whole inner surface of the carpels.

The number of ovules in the ovary, or in its individual compartments, varies considerably; thus, in the Scrophulariaceæ (*e.g.* Snapdragon) and Liliaceæ they are numerous, whilst there are but two in each loculus in the Horse Chestnut and Sycamore, and one only in each compartment in the Umbelliferæ (Fig. 133 D). When there is but one ovule in the ovary it is generally either attached to the base (*e.g.* Persicaria) or suspended from the apex.

In certain families the number of loculi in the ovary increases during the development of the flower, owing to the appearance of what are called *false septa*. In the Cruciferæ (*e.g.* Wallflower), for instance, the bicarpellary ovary is at first unilocular, but becomes bilocular through the formation of a partition joining the two parietal placentas (Fig. 133 F). Similarly, in the Labiatæ (*e.g.* Dead-nettle, Fig. 173) and Forget-me-not the ovary is bilocular in early stages, but subsequently exhibits four compartments as a result of the ingrowth of false septa, one in each original loculus.

When the ovary is apocarpous the individual carpels commonly show a spiral arrangement and this, as we have seen (p. 232), often extends to the other floral organs (*e.g.* Marsh Marigold, Buttercup). In such spiral flowers a marked transition between stamens and petals is occasionally found, this being very obvious in the White Water-lily, where it is very difficult to draw a hard-and-fast line between the two structures. The same phenomenon is frequently observed in double flowers, where the doubling is due to a replacement of the stamens by petals (*e.g.* cultivated Roses and Pinks).

Similarly, in other cases the bracteoles grade off into the sepals, as for instance in the Lesser Celandine in which the outer members of the perianth are green and exhibit a gradual change to a yellow colour, as we pass towards the middle of the flower. Moreover, the outermost green leaves are sometimes

separated from the others by a short interval and are then plainly recognisable as bracteoles. In the Winter Aconite (Fig. 142) the functions of the calyx are performed by three much-divided bracteoles closely resembling the foliage-leaves

FIG. 142.—Flower of the Winter Aconite (natural size), showing the three divided bracteoles which function as a calyx.

and arising immediately beneath the coloured perianth. This recalls the state of affairs seen in the Wood Anemone in which, however, the three bracteoles are situated some little way below the flower.

At the commencement of our consideration of the flower

(p. 230) we likened it to a compressed shoot, and this analogy is emphasised by certain abnormal flowers, such as the Double Arabis or Mountain Snow ; here, instead of producing essential organs the axis continues to grow, forming a series of successive flowers with short separating internodes, the one within the other and each consisting only of calyx and corolla.

We may conclude our discussion of the flower by a brief consideration of the functions of its essential organs. The ovules contained within the ovary do not, except in rare cases, mature into seeds, unless pollen from the same kind of plant has been deposited upon the stigma at a time when the latter

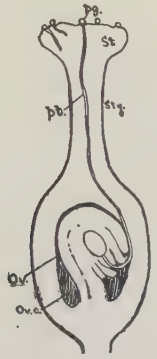


FIG. 143.—Diagram to explain the growth of the pollen-tube and fertilisation ; the ovary contains but a single basal ovule. *Ov.*, ovule ; *Ov.c.*, ovary cavity ; *pg.*, pollen grain ; *pt.*, pollen tube ; *St.*, stigma ; *Sty.*, style.

is still in a receptive condition. By carefully removing the stamens from a number of flowers, before their pollen is shed (*i.e.* in the bud-stage), and then covering each with a bag of fine muslin to prevent access of insects or wind-borne pollen, the necessity of pollen for the formation of seed can be readily shown. For it will be found that flowers treated in this way do not set seed. On the other hand, if pollen from another plant of the same kind is transferred to the stigma of one of the flowers, with the help of a camel's-hair brush, ripe seed will almost certainly be produced.

The transference of pollen to the stigma, in other words *pollination*, is effected in various ways which will form the

subject-matter of the next two chapters. Once on the stigma, each pollen-grain puts out a thread-like tube (the *pollen tube*, Fig. 143, *pt.*) which grows down the style till it reaches the cavity of the ovary and passes into one of the ovules (Fig. 143, *Ov.*). This pollen tube conveys the male fertilising element into the ovule, where it unites (the union being described as *fertilisation*) with the contained female element; the product is a cell which is the offspring of the two parents (the one from which the pollen comes and the other bearing the ovules) and which by subsequent division gives rise to the *embryo* within the seed.

CHAPTER XX

The General Aspects of Pollination

The transference of pollen from the stamens to the stigma is, as we have seen, nearly always essential for the production of seeds. Experiments have, however, also proved that in many plants a larger number of seeds and frequently more vigorous offspring are produced, if fertilisation is effected by pollen from the flower of a different individual. When this latter is the case we speak of *cross-pollination*, whereas the term *self-pollination* is used when the pollen comes either from another flower of the same individual or from the stamens of the self-same flower, the former alternative being however more beneficial than the latter. The advantage of cross- as compared with self-pollination is very apparent in some plants ; for instance, Darwin found that the weight of Cabbages produced from seeds, formed as a result of cross-pollination, was very much greater than those grown from seeds which had been produced by self-pollination, the former varying between 74 and 130 ounces, the latter between 11½ and 46 ounces.

In view of such facts it is not astonishing that a very large number of plants have developed devices which tend to favour cross-pollination. Most flowers contain both stamens and ovaries—in other words, are *hermaphrodite* (indicated briefly by the symbol ☿), but the two kinds of organs rarely ripen at exactly the same time. In some cases the stamens ripen first (*protandrous* flowers), whereas in others the stigma matures before the pollen is shed (*protogynous* flowers). There are, however, all transitions from flowers in which the essential organs ripen almost simultaneously (*e.g.* White Dead-nettle) to flowers in which the one kind of organ has withered before the other is mature. Thus, extremely protandrous flowers are seen in the

Canterbury Bell and Rose-bay Willow-herb (Fig. 144), whilst marked protogyny is exhibited by the Figwort (Fig. 140) and Plantain (Fig. 128).

The tetramerous flower of the Willow-herb has eight stamens and a four-lobed stigma, but until the stamens have finished shedding their pollen (*i.e.* until the male or staminate stage is over) the stigmatic lobes remain closely pressed together, so that their receptive surfaces are not exposed (Fig. 134 ♂). When the stamens wither, the four lobes of the stigma curl back

FIG. 144.—Flowers of Rose-bay Willow-herb, to illustrate protandry (natural size). In the upper flower the stamens are alone mature; in the lower one they have withered, whilst the four stigmatic lobes are now spread out. *st.*, stigma. ♂, male stage; ♀, female stage.

(Fig. 144 ♀, *i.e.* we now enter on the female or pistillate stage), ready to receive pollen from some flower which has opened at a later date. In the spike of the Plantain (Fig. 128) the lower flowers open first and exhibit a white feathery protruding stigma, but at this stage no stamens are to be seen; as the flowers in the upper part of the inflorescence develop, the stigmas of the lower ones wither and their place is taken in each flower by the four stamens. Since the flowers in the female stage (Fig. 128 ♀) are always above those in the male (Fig. 128 ♂), the pollen in falling cannot effect pollination.

In all such extreme cases self-pollination is obviously prevented in the earlier stages of flowering, although we shall find that a considerable number of these flowers make provision for self-pollination just before fading. If however, prior to this, cross-pollination has taken place, pollen from the same flower is ineffective. In fact, in quite a large number of cases (*e.g.* the ordinary flowers of the Dog Violet, many Leguminosæ) such pollen has no effect at all, these forms being spoken of as *self-sterile.*

Still greater certainty of cross-pollination is ensured, when stamens and ovaries occur in distinct flowers which are then said to be *unisexual.* The flowers of the two sexes are either found on the same individual (*e.g.* Hazel, Fig. 129, Birch), when the latter is said to be *monœcious,* or on different individuals (*e.g.* Stinging Nettle, Dog's Mercury, Fig. 134, Willow, Fig. 166, Black and White Bryony, Valerian), when they are described as *diœcious.* Particularly in the latter case self-pollination is out of the question. Not uncommonly such unisexual flowers show remains of the other essential organ and so betray their derivation from an hermaphrodite condition. Thus, in the male (staminate) flowers of the Buckthorn a rudimentary ovary surmounted by a style can be recognised at the base of the perianth-tube.

In such cases we could regard the male flower as an extremely protandrous one in which the female stage is never reached, and a similar explanation could be applied to female (pistillate) flowers. Quite a large number of plants possess unisexual flowers side by side with hermaphrodite ones. Thus, in the Ragwort (Fig. 145), Daisy, and other similar members of the Compositæ the outermost flowers (*ray-florets*) with a strap-shaped corolla are female (Fig. 137 F, Fig. 145 B), whilst those occupying the greater part of the capitulum (*disc-florets*) and having tubular corollas are hermaphrodite and protandrous (Fig. 145 C, Fig. 135 E). In the Coltsfoot, however, the disc-florets are male, having but a rudimentary ovary, whilst the ray-florets are, as before, female. It may be added that in certain groups of flowering plants all sorts of variations in the distribution of sexes are to be found. In the Campion for instance, male, female, and hermaphrodite flowers occur on distinct plants, whilst in the Ash all three types may be borne on the same individual.

Amongst minor devices that tend to favour cross-pollination we may mention extrorse dehiscence of the stamens (p. 241) and the arrangement of the anthers at a lower level than the stigma in many upright flowers or *vice versa* in hanging ones. Many irregular flowers are highly adapted to this end (see next chapter).

Pollen can be conveyed from the stamens to the stigma by various agencies, the commonest being insects, wind, and more rarely water.[1] We may first consider wind-pollination or, as it

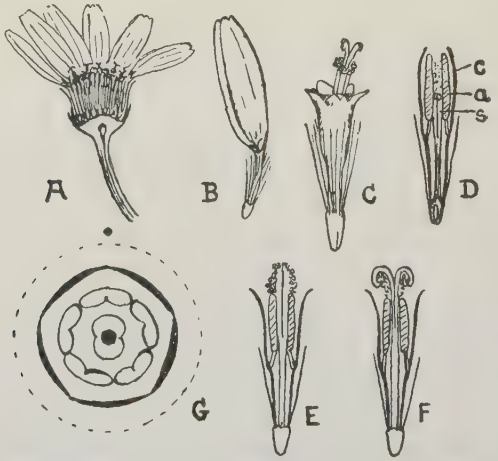


FIG. 145.—Floral structure and pollination in the Marsh Ragwort (A, natural size, other figures somewhat enlarged). A, Capitulum in longitudinal section. B, Ray-floret. C, Disc-floret in early female stage. D, Ditto, in longitudinal section, in early male stage. E, Ditto, with style just emerging. F, Ditto, late stage. G, Floral diagram of disc-floret.

is often called, *anemophily*, a mode of transference occurring frequently amongst simple types of flowers, particularly unisexual ones. It is evident that this mode of pollination depends largely on chance and therefore, if it is to be successful, a much greater amount of pollen must be produced than is necessary to effect fertilisation. We consequently find that wind-pollinated plants either have numerous stamens in their flowers (*e.g.* Poplar, Elm, Hornbeam), or relatively large anthers producing

[1] Water as an agent of pollination is dealt with on p. 339.

copious pollen (*e.g.* Grasses, Fig. 178 A, Pondweeds, Fig. 139*), or the male flowers are greatly in excess of the female ones (*e.g.* Hazel, Scotch Fir). Moreover, the stigma is frequently richly branched and feathery (*e.g.* Grasses, Fig. 178 A, Hazel, Fig. 129 ♀), so that pollen is the more easily caught.

It is further essential that the pollen of anemophilous plants should be readily shaken out of the flowers by the wind; and we may relate to this the frequent occurrence of loose hanging inflorescences (*e.g.* Birch, Hazel, Fig. 129 ♂, and Stinging Nettle), or of anthers which are loosely hinged on long projecting filaments, so that they are moved by the least breath of wind (Grasses, Figs. 139 D and 178 A, Salad Burnet, Plantain, Fig. 128). The pollen itself is dry and powdery in character and usually has a smooth surface, so that there is no tendency for the grains to cling together, thus facilitating a wider distribution.

The flowers of wind-pollinated plants are usually green and inconspicuous, either possessing a simple perianth (*e.g.* Dog's Mercury, Fig. 134, Salad Burnet, Stinging Nettle) or being naked (*e.g.* Ash). They naturally lack all those attractive mechanisms which are so marked a feature of the insect-pollinated flower and to a discussion of which we shall now turn.

The first features to be noticed in such *entomophilous flowers* are the devices which induce insects to visit them. Most important among these is the production of honey in special glands called *nectaries* which may be situated on almost any part of the flower, generally near its base. Very commonly (*e.g.* Pansy, Fig. 155 A, many Leguminosæ) dark lines, known as *honey-guides*, are found upon the petals converging towards their base, *i.e.* towards the point where the honey is formed; these have been thought to indicate the position of the latter to the pollinating insect.

The nectaries are frequently located at the base of the carpels (*e.g.* Marsh Marigold), often on an enlargement of the thalamus known as a *disc* which may either extend equally all around the ovary (*e.g.* the Rue, Fig. 146 B, *n*, Heath) or be more or less confined to its anterior side (as in many Labiatæ and Scrophulariaceæ). In flowers with an inferior ovary (p. 232) the honey-disc is situated on the top of the latter (*e.g.* Umbelliferæ, Fig. 146 E, *n*; Bedstraws). Many members of the Liliaceæ (*e.g.* Tulip) develop nectaries in the wall of the ovary itself, these

appearing as narrow slits when the latter is cut across. In other cases the nectaries are produced on the expanded bases of the stamens, as in the Stitchwort (Fig. 146 C, *n*) and other Caryophyllaceæ, as well as in the Cruciferæ.

The corolla, particularly among the Ranunculaceæ, may also be the seat of honey-formation; in the different members of this family we get all conditions between petals with a

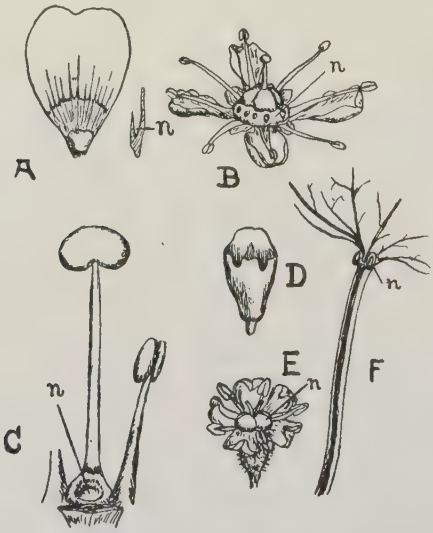


FIG. 146.—Forms of nectaries (A, B, and F, natural size, other figures enlarged). A, Petal of Buttercup, showing flap covering nectary; the right-hand figure the same in longitudinal section. B, Flower of Rue. C, Stamens of Stitchwort. D, Honey-petal of Hellebore. E, Flower of Hogweed. F, Part of leaf of Guelder-rose, showing extrafloral nectaries. *n*, nectaries.

nectary at the base, protected by a small flap (Buttercup, Fig. 146 A), and little trumpet-shaped structures (as in the Christmas Rose, Fig. 146 D, and Winter Aconite, Fig. 142) situated just outside the stamens. The bases of the perianth-members in the flowers of the Crown Imperial likewise bear honey-glands, each appearing as a large circular excavation.

Nectaries often produce such large quantities of honey that it overflows from the depressions in which it is secreted and may

in some flowers accumulate in special *honey-bags*. These are but slightly developed in the Wallflower (Fig. 147, *b*) and other Cruciferæ, where they are formed by the pouch-like bases of the lateral sepals situated opposite the two short stamens bearing nectaries. In other cases, however, they appear as tube-like outgrowths of the perianth or *spurs* (*e.g.* Larkspur, Pansy, Fig. 155 A, *sp.*, Toadflax, Garden Nasturtium, Fig. 135 A). The spur may, however, not merely function as a receptacle for honey, but may actually produce it at its tip ; this is seen in Orchids (Fig. 156 B, *sp.*) and in the Columbine, each petal of the latter being prolonged into a spur. In such flowers a special outgrowth has developed for the purpose of producing honey, and a similar feature can be observed in the Pansy (Fig. 155 A and B, *n*) and Larkspur in which two processes, from the stamens and petals respectively, project into the spur and secrete honey into it.

In a few plants (*e.g.* Guelder-rose, Tare, Black Bindweed, Laurel, Cherry) so-called *extrafloral nectaries* are met with on the vegetative organs, generally on the leaves. Thus, in the Guelder-rose and Cherry (Fig. 146 F, *n*) they appear as little shallow cup-shaped projections on either side of the petiole, whilst in the Tare and Broad Bean they constitute dark depressions on the under surfaces of the stipules.

Nectaries in all cases produce a sweet sugary fluid which at first is very concentrated (being thick and syrupy), but subsequently becomes more and more diluted by absorption of liquid from beneath. We can imitate this mechanism in a simple way by scooping out two hollows in an unpeeled Potato and filling one of them with powdered sugar. After about an hour the latter cavity will be found full of syrup which may even overflow, whilst the other is dry and empty. The sugar has drawn water out of the cells of the Potato in much the same way as the root-hairs take up moisture from the soil. In this manner extrafloral nectaries may serve to get rid of an excess of water in the plant. Similarly, when nectaries are situated on the bases of the stamens (Fig. 146 C), they appear to bring about the drying up and consequent dehiscence of the anthers by withdrawing moisture from the latter, since such stamens have been found to exhibit opening of the anthers, even in a saturated atmosphere.

Not all entomophilous flowers, however, produce honey, a limited number providing no other bait than pollen. Such *pollen-flowers* (*e.g.* Clematis, St. John's Wort, Rock Rose, Poppy) usually possess a large number of stamens, so that there is sufficient pollen, both for pollination and for the purposes of the insect. It may be added that, even in flowers having nectaries, insects generally take a certain amount of the pollen as food.

Many flowers exhibit devices by means of which honey and pollen are protected from the injurious effects of dew or rain. The simplest method of pollen-protection is for the dehisced anther to close up more or less completely, when the air becomes damp (cf. p. 241). The closing of flowers or capitula at night (p. 222) serves to shield both honey and pollen, and the same end is attained by the hanging position occupied by many flowers (*e.g.* Harebell, Fig. 137 A, Heath, Lily of the Valley). The individual flowers in many catkins (*e.g.* Hazel, Fig. 129 *δ*) are protected by the bracts which appear as roofs above them, whilst in forms such as the Buttercup the nectaries are covered by scales arising from the petals (Fig. 146 A). A considerable number of other devices of a similar kind will be described in the subsequent matter.

In addition to nectaries and pollen the colours and odours of flowers constitute sources of attraction. As a general rule the perianth provides the *attractive apparatus*,[1] but sometimes stamens (*e.g.* Willows, Meadow Rue, Old Man's Beard) or even bracteoles (*e.g.* some cultivated Sages, the Bougainvilleas) may play a part. A great feature in plants possessing small flowers is the massing together of the latter, whereby a conspicuous inflorescence is formed (as in Cruciferæ, Umbelliferæ, Compositæ, Fig. 145 A, Elder, and Bedstraws). In many such cases moreover, where the inflorescence is flat-topped, the outermost flowers are irregular and exhibit a one-sided enlargement of the corolla tending to produce greater conspicuity, a feature which is well illustrated by the Candytuft (Fig. 146*), Hogweed, Daisy, etc.; not uncommonly these flowers are unisexual

[1] The importance of the perianth in this respect may be shown by removing all the petals from one specimen of a certain plant, out of doors, and noting the behaviour of insects in relation to it, as compared with a normal plant.

(many Compositæ, p. 253 and Fig. 145 B) or altogether devoid of essential organs (*i.e.* are *neuter*, as in the Guelder-rose and Cornflower, Fig. 175 B), so that they are purely attractive in function.

Since, provided they are visited, pollination is almost a certainty in entomophilous flowers, particularly those frequented by Bees and Humble-bees, a much greater economy in pollen can be effected than in anemophilous plants. As a consequence there is usually (except in pollen-flowers) a relatively small number of stamens, a feature which becomes the more marked the more perfect the mechanism for pollination. The pollen itself generally has a rough or sticky coat, so that it readily adheres to the insect's body, whilst the stigma is not as richly branched

FIG. 146*.—Inflorescence of the Candytuft (natural size), showing the enlarged marginal flowers.

as in most wind-pollinated forms, but has a very sticky receptive surface.

The insects which most frequently act as pollinating agents are the various types of Bees and Humble-bees, Butterflies, Moths, and many different kinds of Flies and Beetles. All of them, except Beetles, possess a special sucking organ, the tongue or *proboscis*, arising from the under side of the head and of very diverse length, being very short in Flies and exceptionally long in Butterflies and Moths, where it is coiled up when not in use. When visiting a flower the position taken up by an insect depends largely on the length of its proboscis and the situation of the nectary. In fact, flowers possessing a long narrow corolla-tube (Fig. 132 B) or a spur are not accessible for honey to any but long-tongued insects, whilst wide open flowers (Fig. 132 A)

provide honey for a variety of visitors, both with long and short probosces. Certain insects (*e.g.* the small Bumble-bee), however, not uncommonly puncture the base of the corolla-tube, when this is too long for them to reach the nectary by legitimate means, and thus steal honey without effecting pollination.

In the majority of cases the insects concerned actually alight on the corolla or perianth, although many Moths hover in front of the flowers they visit. As a result of the different, though for the same flower usually constant, positions taken up by pollinating insects very diverse parts of the body (viz. proboscis, head, back, or abdomen) may become dusted with pollen, and it is of importance in this connection that these are often covered with hairs to which the pollen readily adheres. Sooner or later the stamens and stigma in any given entomophilous flower come to occupy similar situations, so that the pollen taken from the anthers of one flower will be likely to get rubbed against the stigma of another.

The simplest kinds of *pollination-mechanisms* are seen in regular flowers, amongst which two principal types can be distinguished. As the first, we have flowers with a wide open and shallow corolla (*e.g.* Buttercup, Fig. 132 A, Stitchwort, Fig. 168 B, most Rosaceæ) and from these almost any insect-visitor can obtain honey. In such forms the insect alights either on the corolla or on the essential organs (*e.g.* Buttercup, Fig. 132 A), so that either its head or its under side becomes dusted with pollen. Flowers of this type are often visited by small insects which may in their erratic wanderings effect pollination, although no doubt it is often only pollen from the same flower that is transferred. In the case of umbels, corymbs, and capitula, insects commonly crawl about on the flat top of the inflorescence and, since many of the plants concerned are markedly protandrous, pollen gets transferred from the younger flowers in the centre to the older ones near the edge, features which are well seen in the Hogweed.

The second type of regular flower, the *tubular* one, possesses a perianth-tube of varying length and formed in one of two ways. Most usually, as in the Primrose (Fig. 148) and Narcissus (Fig. 132 B), the corolla or perianth is gamopetalous, their

united portions producing the tube. But where the petals of a polypetalous corolla have long claws (Fig. 136 A) they, together with the upright sepals, may likewise give rise to a tube; the calyx in this case is either polysepalous, as in the Cruciferæ

FIG. 147.—Flower of the Wallflower, showing the tube produced by the four upright sepals and the claws of the petals (natural size). *b*, one of the pouched sepals serving as a honey-bag.

(Fig. 147), or gamosepalous, as in the Campion (Fig. 168 A) and Pink. In all such forms the expanded ends of the petals constitute the alighting platform (Fig. 132 B) and the pollen is brushed off either on to the proboscis or the head of the

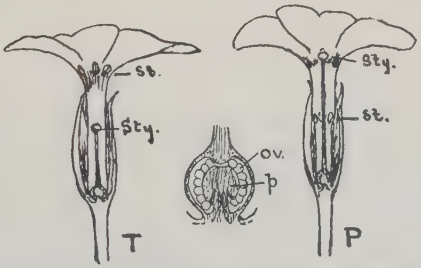


FIG. 148.—Floral structure of Primrose, showing longitudinal sections of thrum-eyed (T) and pin-eyed (P) forms (natural size). *St.*, stamens; *Sty.*, stigma. The middle figure shows the ovary in longitudinal section and considerably enlarged. *ov.*, ovule; *p*, free central placenta.

pollinating insect, according to the level at which the anthers stand in the tube. Such flowers are visited only by long-tongued insects, the variety of visitors becoming the more restricted the greater the length of the tube.

A special device, spoken of as *heterostyly* and tending to

favour cross-pollination, is seen in the tubular flowers of the Primrose (Fig. 148), Water Violet, and Purple Loosestrife, in all of which more than one type of flower is produced (two in the first two cases, three in the last), the difference consisting in the relative lengths of the essential organs. Thus, in the Primrose some individuals have the stigma situated at the mouth of the corolla-tube (pin-eyed form), the stamens occupying a position half-way down (Fig. 148 P), whilst in others the relative positions of stamens and stigma are reversed (thrum-eyed form, Fig. 148 T). As a consequence the pollen received upon the proboscis from a flower of the pin-eyed type will only be at the appropriate level for effecting pollination in one of the thrum-eyed type and *vice versa*.

CHAPTER XXI

Special Mechanisms for Pollination

A more perfect pollination-mechanism, than that of the flowers considered at the end of the previous chapter, is found in those having an irregular corolla, a device which usually results in a greater restriction of insect-visitors. In such flowers the agent is compelled to take up a definite position with reference to the essential organs and must frequently be strong enough to force open the more or less closed corolla. Irregular flowers in addition often show excellent devices for the protection of pollen and honey. In studying the relation between flower and insect in such cases the relative sizes of the two must be carefully considered, and the reader is advised to devote a few hours on some summer's day to observing the kinds of insects visiting these flowers (see Appendix XXIII.).

As a first example the *papilionaceous flower* of British Leguminosæ may be studied. Here the corolla (Fig. 150 A, cf. also Fig. 133 C) consists of the following parts: (i) a large posterior petal, the standard, in most cases placed almost vertically (Fig. 150 A and C, *s*); (ii) a pair of wings (*w*) situated at the sides; and (iii) a pair of anterior petals, more or less joined together to form a boat-shaped structure, the keel (*k*). The essential organs are completely enclosed within the keel (see Fig. 151 E) and are thus efficiently protected; they consist of ten stamens (cf. Fig. 133 C), often of two lengths, the filaments forming a tube (p. 244) around the central pod-like ovary which is provided with a long style ending in a stigma of varied character (Fig. 151 D, *St.*). Honey is usually produced on the inner sides of the bases of the filaments and accumulates in the trough formed by them. In such honey-producing flowers the posterior stamen is always free (cf. Fig. 133 C), thus leaving

a space in the stamen-tube for the insertion of the proboscis of an insect. Some members of the Leguminosæ (*e.g.* the Broom, Rest-harrow, Lupine), however, produce no honey (*i.e.* are pollen-flowers, p. 258) and in them all the ten stamens are united (cf. Fig. 170 of the Needle Furze).

The standard constitutes the principal attractive mechanism of the flower, whilst the wings form the alighting platform, the head of the insect being directed towards the standard. Since obviously neither honey nor pollen are easily reached, these flowers can only be visited with profit by sufficiently intelligent

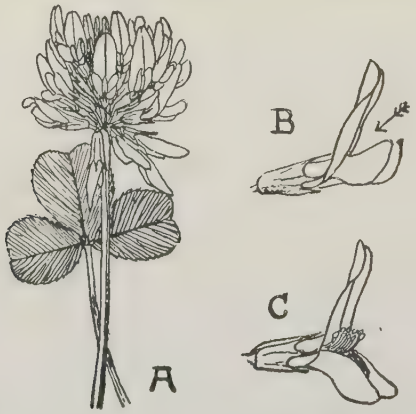


FIG. 149.—Pollination in the Clover (A natural size, B and C enlarged). A, Inflorescence and leaf. B, Single flower seen from the side, in its normal condition. The arrow indicates the direction of approach of the pollinating insect. C, The same, showing position of parts at time of pollination when wings and keel are depressed.

insects and by such as are heavy enough to expose the essential organs; Bees fulfil both requirements and are indeed amongst the commonest visitors. The base of each wing is provided with an outgrowth which fits into a hollow in the adjacent petal of the keel (Fig. 150 D) and thus, when a Bee alights on the wings, these and the keel get depressed simultaneously. As a result the essential organs are exposed and rub against the *under surface* of the insect's body (cf. Fig. 149 B and C). Although the stigma is often surrounded by pollen, as it lies hidden in the keel, self-pollination does not occur owing to self-sterility (p. 253) and to the stigma being unreceptive until it has been

rubbed. If therefore the insect already bears pollen from another flower, it will effect cross-pollination at the same moment as its body rubs against the stigma. When it flies away, the parts of the flower return to their original positions and the keel again screens the essential organs. This, the simplest

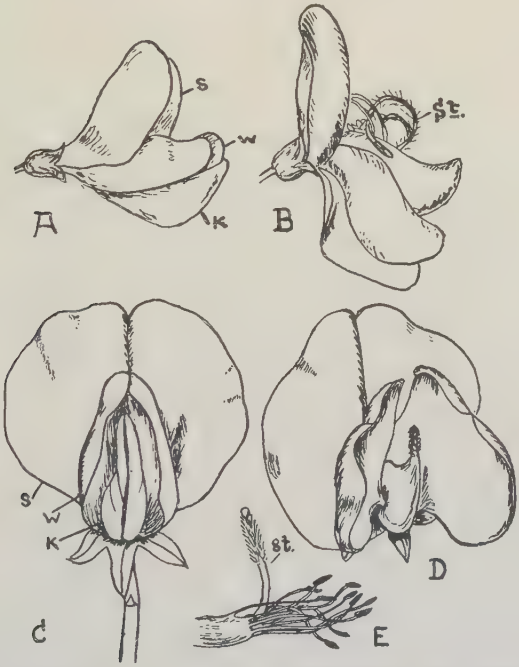


Fig. 150.—Pollination in the Broom and Sweet-pea (natural size, E enlarged). A, Flower of Broom before pollination, seen from the side. B, Ditto after pollination. C, Flower of Sweet-pea, seen from the anterior side. D, Ditto with stigma and stylar brush emerging, as during pollination. E, Essential organs enlarged, showing position when released from keel. *k*, keel ; *s*, standard ; *st.*, style ; *w*, wings.

type of pollination-mechanism in Leguminosæ, is seen in the Clover, Sainfoin, and Melilot, but many of the other members show modifications which will now be considered.

In the Sweet-pea, Everlasting Peas, and Vetches the style, just beneath the small stigma, bears a dense brush of hairs (Fig. 150 E, *st.*) upon which the pollen is shed. The tip of the

keel in the Sweet-pea is prolonged into an upright beak (Fig. 150 D) in which are situated the anthers of the ten stamens, surrounding the stigma and stylar brush. When a Bee alights on the wings and the keel is depressed, the style emerges (Fig. 150 D) brushing out the pollen onto the insect's under surface, whilst the stamens remain concealed; the relative positions of style and stamens are now approximately as in Fig. 150 E.

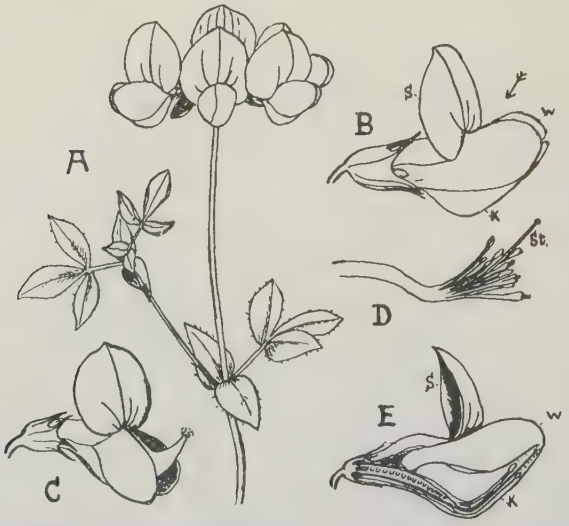


FIG. 151.—Pollination in the Bird's-foot Trefoil (A natural size, B–E enlarged). A, Portion of plant with inflorescence. B, Side-view of flower before pollination; arrow marks direction of approach of insect. C, Flower during pollination, showing emergence of pollen. D, Essential organs. E, Longitudinal section of flower. *k*, keel; *s*, standard; *St.*, style; *w*, wings.

When the insect flies away, the style again becomes enclosed in the keel and the flower can be visited afresh.

In the Lupine, Rest-harrow, and the Bird's-foot Trefoil (Fig. 151) the two petals of the keel are not only joined in the customary manner along their lower edges, but for some distance along their upper edges also, leaving, however, a small circular opening near the pointed tip (Fig. 151 C and E). The tops of the filaments of the five longer stamens are swollen up (Fig. 151 D), so as to form collectively a piston or ramrod by means of which

the pollen collecting in the tip of the keel is forced out of the opening, when the keel is depressed (Fig. 151 C). The style is appreciably longer than the stamens, so that the stigma is the first to protrude, when an insect alights on the flower. As in the previous cases, the different parts return to their normal position when the visitor flies away.

As a last example of pollination in Leguminosæ the so-called *explosive flowers* of the Broom (Fig. 150 A and B), Needle-furze, and Gorse may be described. In these the style and stamen-tube are compressed into a relatively small keel so that, when an insect of sufficient weight alights on the wings, the consequent depression of the keel leads to a sudden release of the confined essential organs; the latter therefore emerge with a jerk and a shower of pollen is sent over the visitor. In this case no return of the floral organs to their previous positions takes place, when the insect flies away; the flower is "exploded" and stamens and stigma remain projecting from it (Fig. 150 B).

The pollination of the Broom is so far exceptional among British Leguminosæ in that some of the pollen is deposited *on the back* of the insect. When the latter alights, the five shorter stamens first emerge and strike its under surface, but immediately afterwards the five longer stamens and the stigma spring out (Fig. 150 B) and strike the insect's back. It will be perceived that the pollen received by the lower side of the body in this case cannot be effective for pollination and probably serves as food.

In the Labiatæ and in many Scrophulariaceæ the pollen is regularly deposited *on the back* of the insect. The usually horizontal flowers of most members of the former family exhibit a longer or shorter corolla-tube (Fig. 137 D), the upper part of which is drawn out into a helmet-shaped hood (*h*), formed by the two posterior petals and constituting a roof over the four stamens and the bilobed stigma. The anterior part of the corolla is enlarged to form an alighting platform (*p*), whilst projections (*l*) on either side of the throat give a hold to the fore-feet of the insect during pollination. Honey is secreted by a disc (p. 255) at the base of the ovary but, owing to the presence of a corolla-tube, can only be reached by long-tongued insects, such as will have a body sufficiently large to fill the space between the upper and lower lips. Frequently hairs are present in the

upper part of the tube, these serving to prevent the intrusion of small insects which would steal honey without effecting pollination. In probing the nectary the visitor brings his back into contact with the essential organs and thus effects pollination. The flowers are commonly protandrous, the stamens first projecting downwards to a slight extent so that they are bound to touch legitimate visitors, the stigma at this stage being above them and with its two lobes pressed together; subsequently the latter diverge and the stigma comes to lie a little below the position previously held by the stamens.

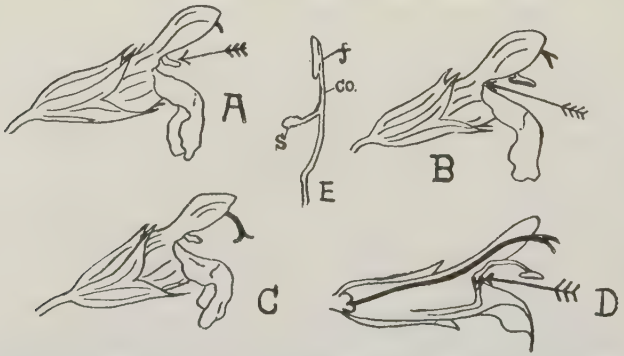


FIG. 152.—Pollination in the Garden Sage (all figures natural size). A, Flower before pollination, in male stage. B, Flower during pollination. C, Female stage. D, Flower in longitudinal section showing mode of pollination. E, Single stamen (slightly enlarged). The arrows show direction of approach of pollinating insect. *co.*, connective; *f*, fertile lobe; *s*, sterile lobe of stamen.

An interesting modification is seen in the Garden Sage (Fig. 152) whose flowers have only two stamens, each with a much elongated connective joining the two anther-lobes (cf. p. 242 and Fig. 152 E, *co.*). One arm of the connective is somewhat longer than the other, and the anther-lobe at the end of the short arm is sterile (*i.e.* produces no pollen). These sterile lobes are so placed in the throat of the corolla-tube that an insect probing for honey must push against them (Fig. 152 A and D), thus bringing the fertile lobes down upon its back (Fig. 152 B). In the female stage the stigma projects to a very marked extent (see Fig. 152 C), so that its lobes are bound to touch the back of an insect-visitor.

Amongst the Scrophulariaceæ we have in the first place flowers with a pollination-mechanism very similar to that of Labiatæ (*e.g.* Foxglove, Fig. 137 E, Red Eyebright, Fig. 73 A), although the shape of the corolla is often different. The same type of construction is seen also in the flowers of the Musk, the sensitive stigma of which (cf. p. 221) is a special device that prevents self-pollination. The folding together of the two lobes (Fig. 125 B) is brought about by contact with the pollen-bearing proboscis of an insect, cross-fertilisation

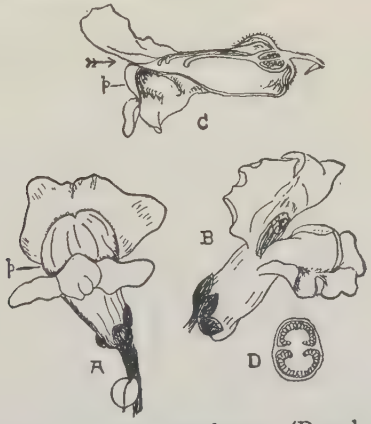


FIG. 153.—Pollination in the Snapdragon (D enlarged, other figures about two-thirds natural size). A, Complete flower seen from the anterior side. B, Flower in side-view, with the corolla forced open to display the essential organs beneath the upper lip. C, Flower in longitudinal section. The arrow marks the direction of approach of the insect. D, Cross-section of ovary, showing the large axile placenta. *p*, pouch formed by lower lip of corolla.

being thus accomplished; since the stigma remains closed for some little time, there is no chance of its getting dusted with the flower's own pollen when the insect withdraws.

The Snapdragon (Fig. 153) and Toadflax are peculiar in the fact that the mouth of the corolla is completely closed by a pouch-like outgrowth from the lower lip (Fig. 153 A and C, *p*). In this way pollen and honey are not only amply protected from outside moisture, but the flower is alone accessible to insects (*e.g.* Bumble-bees) which are strong enough to force open the aperture to the corolla-tube. The Toadflax differs from the

Snapdragon in the possession of a long spur (cf. Fig. 120), functioning as a honey-bag, whereas in the latter the anterior part of the corolla-tube is merely a little enlarged to hold the honey (Fig. 153 B and C).

A third type of Scrophulariaceous flower is illustrated by the Figwort (Fig. 140) which we have already noticed as an example of marked protogyny (p. 252); here the stigma (♀) and stamens (♂) successively occupy positions against the lower lip, so that the under side of the insect (often a Wasp) is effective in pollination.

Further examples of special pollination-mechanisms exhibited by irregular flowers are furnished by the Monkshood, Pansy,

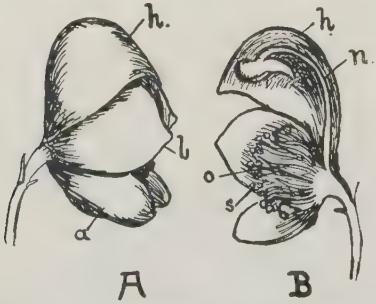


FIG. 154.—Flowers of the Monkshood (natural size). A, Entire flower seen from the side. B, Flower in longitudinal section. *a*, anterior member; *h*, hood (posterior member); *l*, lateral member; *n*, nectary; *o*, ovary; *s*, stamens.

and Orchids. In the first, each flower has a petaloid (*i.e.* coloured) perianth composed of a large hood-like posterior member (Fig. 154, *h*), overlapping the two lateral ones (*l*) which in their turn project over the anterior pair (*a*). Within the hood are situated two long-stalked nectaries (Fig. 154 B, *n*), whilst the essential organs consist of numerous stamens (*s*) and an apocarpous ovary (*o*). The insects (Humble-bees) alight on the lateral and anterior members of the perianth and probe for honey beneath the hood, so that their under side becomes dusted with pollen in the first (male) stage of the protandrous flower. Subsequently the stamens curl right back, so that in the female stage the stigmas touch the Bee's abdomen and may thus be cross-pollinated.

In the Pansy (Fig. 155) the anterior petal (*a*) serves as the landing-place for the insect, which then pushes its proboscis (the arrow in Fig. 155 A) into the honey-bag formed by the spur (*sp.*, cf. p. 257). The five stamens have very short filaments and, by means of their prolonged connectives (Fig. 155 B, *c*; p. 242), fit close together around the style, a little way beneath the stigma. The actual receptive portion of the latter is situ-

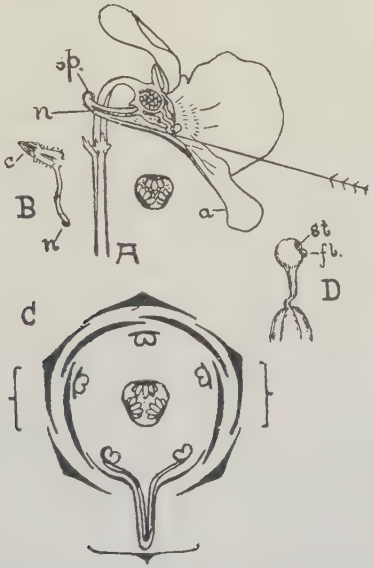


FIG. 155.—A–C, Structure of flower of Pansy. A, Longitudinal section of flower (natural size). B, Single stamen (enlarged). C, Floral diagram. D, Ovary, etc. of Field Pansy (enlarged). *a*, alighting platform; *c*, connective of anther; *fl.*, flap below stigmatic surface; *n*, nectary; *sp.*, spur; *st.*, stigma.

ated on its anterior face (*st.*) and is constituted by a small hollow which is covered by a flap (*fl.*) hinged towards the base of the flower (Fig. 155 D). The pollen is shed on to the proboscis of the insect and, in the withdrawal of the latter, the flap over the stigmatic surface is closed, so that self-pollination in these flowers is impossible. When visiting another flower the insertion of the proboscis pushes back the flap and the pollen is thus deposited on the stigmatic surface.

Many British Orchids show a spurred flower with a very complex mechanism, and we may take the Early Purple Orchis (Fig. 156) as an example. The irregular perianth here consists of two whorls, each of three members (cf. Fig. 156 C), the posterior petal (*labellum*) of the inner series forming an alighting platform (*l*) and being drawn out into a long spur (*sp.*). Owing to the

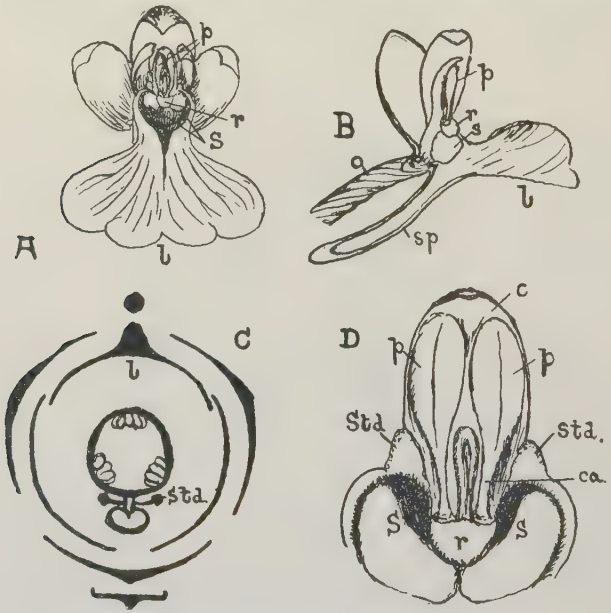


Fig. 156.—Structure of flower of Early Purple Orchis (A and B somewhat enlarged, D considerably magnified). A, Entire flower, seen from the front. B, Flower in longitudinal section, except for ovary which is shown entire. C, Floral diagram. D, Column with essential organs. *c*, column ; *ca.*, stalk of pollinium ; *l*, labellum ; *o*, ovary ; *p*, pollinium ; *r*, pouch ; *s*, stigma ; *sp.*, spur ; *Std.*, staminode.

twisting of the sessile flower through half a circle, in the course of its development, the labellum, however, comes to occupy an anterior position, the twisting being very apparent if one examines the inferior ovary (*o*) which is elongated and resembles a flower-stalk. The remaining five petals are grouped so as to form a protective hood over the essential organs (Fig. 156 A and B). The latter (Fig. 156 D) occupy the centre of the flower

and are situated on a short column (*c*), the upper part of which bears a single large stamen with two very distinct anther-lobes, each containing a coherent mass of pollen-grains (a so-called *pollinium*, *p*). The pollinia are continued below into short stalks (*ca.*) which end in little sticky swollen discs; these are contained in a shallow pouch (*r*) which forms a slight projection on the column, somewhat overhanging the mouth of the spur. Below this pouch, and on either side of it, are seen the two broad flat stigmatic surfaces (*s*) which are more or less joined together. Above them two small teeth, representing barren stamens or staminodes (*Std.*), are distinguishable.

An insect settling on the labellum has to pierce the tissue at the base of the spur for honey and, whilst thus occupied, its head necessarily comes into contact with the pouch (*r*). As a result the sticky ends of the stalks of the pollinia adhere to it and, when the visitor flies away, it carries with it the two pollinia projecting vertically from its head. In the space of half a minute their stalks bend forwards through a right angle, so that from a position like this | they curve into one like this —. When a new flower is visited, the pollinia are therefore at the right level to strike against the sticky stigmas.

The Compositæ exhibit a pollination-mechanism quite different from those hitherto considered. A large number of the plants belonging to this family have capitula with strap-shaped female ray-florets and numerous tubular hermaphrodite disc-florets (p. 253 and Fig. 145 A); but in the Hawkweeds, the Dandelion (Fig. 175 A) and the Chicory, for instance, all the flowers are strap-shaped and hermaphrodite, whilst in the Cornflower all are more or less tubular and, except for the outer neuter ones (p. 259 and Fig. 175 B), each contains both stamens and ovary. As a general rule the hermaphrodite florets alone produce seed and their arrangements for pollination will now be described. The five stamens are introrse and syngenesious (p. 244 and Fig. 145 G), the pollen being shed into the tube formed by the joined anthers (Fig. 145 D). At this stage the two lobes of the stigma are pressed together, with their receptive surfaces in contact, the style as yet being quite short. When the stamens have dehisced the latter commences to grow, so that the pollen gets gradually brushed out of the top of the anther-tube by the numerous hairs on the upper part of the style (Fig. 145 E).

By continued growth the stigma is carried beyond the anthers and soon after its two lobes diverge (Fig. 145 C), thus exposing the receptive surfaces above the mass of pollen that has been swept out of the stamen-tube.

The honey is produced by a nectary surrounding the base of the style and, owing to the relatively short corolla-tube of many forms, the capitula are visited by a variety of insects, chiefly Bees and Flies. These become dusted with pollen on their under surface and, as often as not, merely transfer it from one floret of the capitulum to another. As the flower gets older the lobes of the stigma continue to diverge till they curl right back, as in Fig. 145 F, thus bringing their receptive surfaces into contact with the pollen still adhering to the hairs on the style. In this way self-pollination is assured, if cross-pollination has not already taken place (cf. p. 276).

The different kinds of Bees are by far the commonest insect-visitors to the irregular flowers considered in this chapter, and this applies especially to those which are blue, a colour for which Bees seem to have a decided preference. Owing to the fact that many Bees visit only one kind of flower at a time, they are the most useful agents in insect-pollination. Butterflies, on the other hand, seem to be attracted chiefly by white and red flowers and, where these have a relatively long corolla-tube, these insects may be the most important visitors (*e.g.* Red Campion, Ragged Robin, Bladder Campion). A considerable number of flowers have become markedly adapted to pollination by night-flying Moths (*e.g.* Evening Primrose, Butterfly Orchis, Tobacco, Honeysuckle, Fig. 157, Phlox, Convolvulus, White Jasmine), inasmuch as many only open at night and at this time alone emit a strong scent. Such flowers are mostly white or yellow so that they are relatively conspicuous in the dusk and, since Moths usually hover in front of the flower (p. 260), no alighting platform is necessary and the flowers are frequently regular. The long projecting filaments with loosely hinged anthers seen in the Honeysuckle (Fig. 157) are well adapted to shed pollen on to the body of a hovering Moth.

Any flower which has a sufficiently short corolla-tube (*e.g.* Saxifrages, Speedwells, Enchanter's Nightshade, Forget-me-nots) may be attractive to Flies amongst others, but certain flowers are definitely adapted for pollination by such insects.

These are generally characterised by a fœtid odour and a dirty brown or purplish colour (*e.g.* Fly Orchis, Herb Paris, Cuckoo-pint). In other cases the flowers exhibit deceptive mechanisms, well seen in the Grass of Parnassus which is occasionally found in marshes. Here stamens and corolla are separated by five staminodes, each of which branches into several stalks, the latter terminating in shiny knobs mimicking nectaries.

The arrangements for pollination in the Cuckoo-pint (Fig. 158) are particularly interesting, not only because this plant shows all the characteristics of a fly-visited one, but also because pollination is effected by imprisonment of the insects concerned.

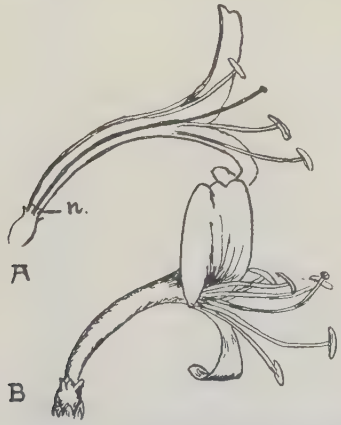


FIG. 157.—Structure of flowers of Honeysuckle (natural size). A, In longitudinal section. B, Entire flower in side-view. *n*, nectary.

The fleshy spike bears the naked unisexual flowers on its lower portion only, those at the very base being female (each consisting of one carpel) and those above male (each with 2 to 4 stamens); beyond these (not quite half-way up the spike) are a number of downwardly curved hairs (*h*) which wither about the time that the stamens shed their pollen. The upper half of the spike is dilated to form a purple club-shaped structure. The whole inflorescence is enveloped in a large sheathing spathe (p. 226), the lower part of which forms a tube narrowing to a kind of waist, at the level where the hairs above mentioned are situated, whilst the upper portion expands into an open leafy structure exposing the swollen tip of the axis (Fig. 158 A).

Small Flies (Midges), attracted by the latter and the evil odour, crawl down into the swollen base of the tube; their escape is prevented by the hairs which will only bend downwards, so that the insects remain imprisoned until these wither. The female flowers are mature some time before the male, so that if the insect bears pollen from another individual it will in its wanderings effect cross-pollination. In escaping the Fly must

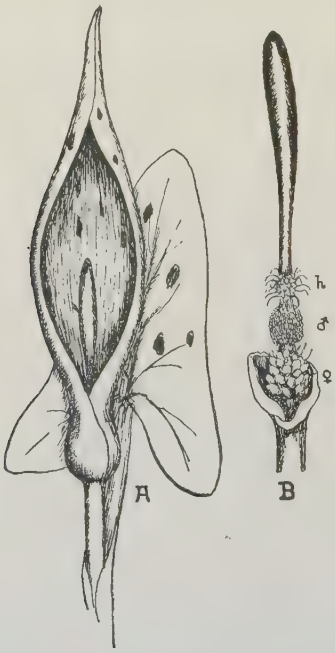


Fig. 158.—Inflorescence of Cuckoo-pint (slightly reduced). A, Leaf with complete inflorescence showing the spathe. B, Spike with spathe removed. *h*, hairs; ♂, male flowers; ♀, female flowers.

pass the stamens of the male flowers which have now dehisced, so that it becomes coated with a fresh load of pollen.

In many flowers, whose construction favours cross-pollination, eventual self-pollination takes place so that fertilisation in one way or another is assured. This feature has already been noticed in Compositæ (p. 274 and Fig. 145 F), but numerous other examples can be found. Thus, in the extremely pro-

tandrous flowers of the Harebell and Canterbury Bell the stamens shed their pollen on the numerous hairs covering the upper part of the style and then wither, after which the lobes of the stigma diverge so that cross-pollination can occur; subsequently they curl right back, as in Compositæ, and become dusted with the pollen on the style. In the Willow-herb the sequence is much the same, except that the stamens persist into the female stage, the backwardly curving stigmas in this instance coming into contact with the anthers themselves.

Certain plants, moreover, produce flowers which are only capable of self-pollination, since they never open. Such *cleistogamic flowers* have no attractive petals and, as pollination is assured, form only very little pollen. The Violet and Wood Sorrel afford good examples, the cleistogamic flowers in these cases being produced after the showy ones (which in the Violet are capable only of cross-pollination, cf. p. 271) and, owing to their short peduncles, remaining hidden amongst the foliage-leaves. They are developed in the summer, when the trees above these woodland-plants have formed a dense crown of foliage, so that the light which reaches them is of relatively low intensity.

Our study of the flower and its various parts has shown us, that the calyx is usually a protective structure that exhibits no great variety of form. On the other hand, the corolla not only renders the flower conspicuous to insects, but in most cases shows obvious modifications to ensure the effectiveness of their visits and the exclusion of undesirables. It is thus mainly the pollinating agency that gives the clue to floral structure, whether the former be insects, wind, or water. In all cases plants developing the most effective mechanism will, as a necessary consequence, set the greatest amount of seed and produce the most offspring. Moreover, the increased certainty of pollination, where insects are the transferring agents, allows except in pollen-flowers of a reduction in the number of stamens and the output of pollen—in other words, an economy of material.

CHAPTER XXII

Fruits, Seeds and their Methods of Dispersal

As a result of fertilisation we not only have the production of an embryo within the ovule (cf. p. 250), but the latter also undergoes an increase in size during which its surface-layers harden to form the *testa* or *seed-coat* (p. 25). At the same time the wall of the ovary enlarges and usually becomes either hard and dry, or fleshy, thus giving rise to the fruit-wall or *pericarp*, the fruit itself being described as dry or succulent according to the character of its wall. It will be realised, therefore, that the fruit corresponds to the whole ripened ovary, whilst the seeds are the matured ovules contained within it. When there is any doubt as to the nature of a given structure (*e.g.* in Grasses, where the testa of the single seed is completely joined up with the pericarp, cf. p. 38), a seed can always be distinguished from a fruit by the fact that it exhibits only one scar (the hilum, p. 25), whereas the fruit shows two, one marking the former attachment to the plant, the other the remains of the style.

Where the ovary is syncarpous a single structure develops from it and we have a *simple fruit*, but when the ovary is apocarpous each carpel matures separately and we may speak of the aggregate as a *compound fruit*. Two types of dry fruits may be distinguished, the one usually remaining attached to the parent-plant and splitting open to liberate the contained seeds (dehiscent fruits), whilst in the other the pericarp merely decays away after the fruits reach the ground (indehiscent fruits). Practically all indehiscent fruits are one-seeded, whilst many-seeded ones are dehiscent. The necessity for dehiscence in the latter class is obvious, since otherwise all the seeds would come to germinate at the same point and the offspring would harm one another by mutual competition.

Examples of *dry indehiscent fruits* are furnished by the *achenes* with a membranous, and the *nuts* with a hard woody pericarp. The fruit of Compositæ and Grasses is an achene which is, however, peculiar in the fact that pericarp and testa are fused, whilst that of the Buttercup (Fig. 159, *a*) consists of a collection of achenes. The Hazel and the Acorn provide instances of nuts, each of which is enclosed in a cup formed by bracts and bracteoles, but it may be mentioned that some of

Fig. 159.—Examples of dry fruits (*a* and *d* natural size, *g* somewhat enlarged; others slightly reduced). *a*, Buttercup (collection of achenes). *b*, Monkshood (three follicles). *m*, midrib of carpel; *l.v.*, lateral vein of same. *c*, Tare (legume); lower figure shows pod after dehiscence. *d*, Wallflower (siliqua); right-hand figure shows portion of false septum with seeds. *e*, Snapdragon (capsule with apical pores). *s*, style. *f*, Campion (capsule with teeth). *g*, Plantain (capsule with lid). *h*, Poppy (porous capsule).

the nuts of everyday life (*e.g.* Walnut, see p. 283, Brazil Nut) are not true nuts.

Not uncommonly fruits derived from multilocular ovaries, containing more than one ovule, split along the septa into compartments, each with a single seed and equivalent to as many achenes; such fruits are said to be *schizocarpic*. Thus, in the Umbelliferæ the fruit at maturity splits into two achenes in the way shown in Fig. 160 A, whilst the Labiatæ exhibit

four achenes (Fig. 160 D) produced by an early fission of the ovary, and the Mallow (Fig. 160 C) as many achenes as there were loculi in the original ovary. A similar splitting of the ripe fruit into compartments is seen in the Crane's Bill (Fig. 160 B), but here the contained seeds are subsequently shot out of the opening segments.

The simplest type of *dehiscent fruit* is the *follicle*, seen in the Marsh Marigold, Monkshood (Fig. 159, *b*), etc., in which the dry pericarp formed from a single carpel dehisces along the

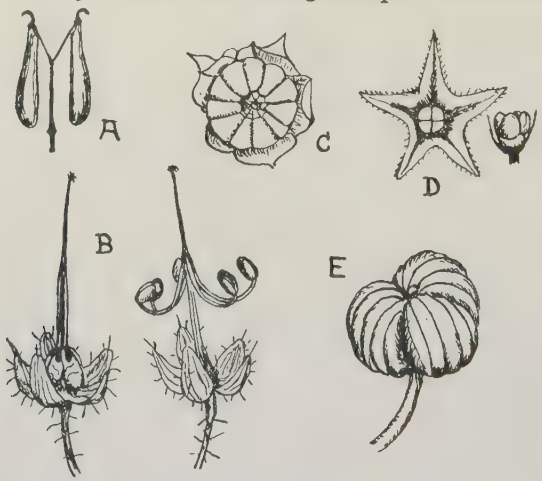


Fig. 160.—Types of schizocarpic fruits (A enlarged, other figures natural size). A, Beaked Parsley. B, Crane's Bill; left-hand figure before, right-hand figure after splitting into achenes. C, Mallow. D, White Dead-nettle; right-hand figure shows fruit, with calyx removed, in side view. E, Garden Nasturtium.

ventral suture (p. 244). This constitutes the most essential difference from the *legume* of Leguminosæ (Fig. 159, *c*) in which dehiscence takes place along both sutures, the two valves often twisting up in the way shown in the figure. A somewhat similar fruit, in this case, however, derived from a bicarpellary ovary, is the *siliqua* characteristic of Cruciferæ (*e.g.* Honesty, Wallflower, Fig. 159, *d*). Here dehiscence takes place along both edges and commences at the base of the elongated fruit, so that as it proceeds the two carpels separate below but remain cohering above. The false septum (p. 247), spread out on a framework

formed by the parietal placentas, remains standing vertically and the seeds attached to the latter (cf. right-hand drawing in Fig. 159, *d*) are gradually shaken off by the wind. Many members of the Cruciferæ have very short siliquas known as *siliculas* (*e.g.* Shepherd's-purse Fig. 4 B) which dehisce in just the same way.

All dehiscent fruits arising from a syncarpous ovary are described as *capsules*, the siliqua just mentioned being a special form of the latter. Capsules differ chiefly amongst one another in the number of compartments and the mode of dehiscence, the former feature depending upon the structure of the ovary. Most commonly opening takes place by longitudinal slits in the pericarp along the dorsal suture of each carpel, *i.e.* the capsule is *loculicidal* (*e.g.* Iris, Willow-herb, Rock-rose), whilst much more rarely the slits appear along the lines of junction of the carpels, when the capsule is *septicidal* (*e.g.* St. John's Wort). In the Caryophyllaceæ and the Primrose the top of the unilocular fruit splits into a number of teeth which curl right back in dry air (*e.g.* the Campion, Fig. 159, *f*), whereas in the Pimpernel, Creeping Jenny, Henbane, and Plantain (Fig. 159, *g*) it breaks off cleanly as a lid. The ripe fruit of the Poppy (Fig. 159, *h*) exhibits a series of pores beneath the flat top (*porous* dehiscence), due to the wall between each pair of placentas curling slightly outwards at these points ; pores are formed in a similar manner at the base of the hanging capsule of the Harebell. In the Snapdragon (Fig. 159, *e*) there are three openings at the apex of the fruit, each of which is surrounded by several small teeth.

The Crane's Bill (cf. above and Fig. 160 B) has shown us that even one-seeded compartments may dehisce to liberate the seed, and the same behaviour is observed in the Horse Chestnut in which the prickly pericarp splits into three valves at maturity. The fruit of this plant, however, sometimes includes two or even three seeds and this explains its dehiscence. The occasional presence of more than one seed is due to the fact that each of the three loculi of the ovary contains two ovules, although as a general rule only one of the six ripens. The majority of indehiscent types are one-seeded from the first, but in some this condition is attained, as in the Horse Chestnut, by all but one of the ovules dying away ; thus the

ovary of the Oak is trilocular with two ovules in each compartment, but five of these invariably fail to ripen, leaving the Acorn one-seeded.

The two principal types of *fleshy fruits*, both indehiscent, are the *berry* and the *drupe*. The former has a pericarp which is fleshy throughout, whilst in the latter the inner part is hard and stony. We can consequently in the berry (Fig. 161 A–B) distinguish between the surface-skin or *epicarp* (*ep.*) and the

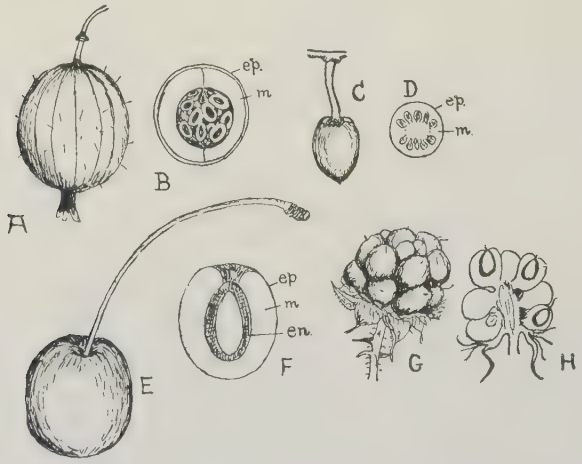


Fig. 161.—Types of fleshy fruits (slightly reduced). A–B, Gooseberry, entire and in cross-section. C–D, Bittersweet (berry), entire and in cross-section. E–F, Cherry (drupe), entire and in longitudinal section. G–H, Blackberry (collection of drupes), entire and in longitudinal section. *en.*, endocarp ; *ep.*, epicarp ; *m*, mesocarp.

fleshy portion or *mesocarp* (*m*), whilst in the drupe (Fig. 161 E–F) we have in addition the hard *endocarp* (*en.*). Examples of berries are furnished by the Currant, Gooseberry (Fig. 161 A–B), Bittersweet (Fig. 161 C–D), and Tomato, the first two having parietal (Fig. 161 B), the last two axile placentas (Fig. 161 D). The Date is a single-seeded berry in which the hard stone is constituted by the endosperm, the actual testa forming the delicate membrane around the latter. Other special kinds of berries are seen in the Orange, Lemon, Grape, Banana, Cucumber, and Vegetable Marrow.

Typical drupes are illustrated by the Plum, Cherry (Fig. 161 E–F), Almond, Peach, etc., whilst the Walnut and Coco-nut are drupes in which, however, the layers outside the endocarp are generally removed before they are placed on the market. The Raspberry and Blackberry (Fig. 161 G and H) furnish instances of compound fruits (p. 278) composed of small drupes.

Whereas berries are generally many-seeded, drupes usually contain but one seed. This is no doubt due to the fact that the hard endocarp renders the drupe equivalent to a nut, from which the seed is only slowly liberated by the breaking down of the stone. On the other hand, the individual seeds of a berry get scattered when the fruit is eaten by animals.

In some plants the fruit is not composed of the ovary alone, other parts of the flower (especially the receptacle) participating in its formation, and when this is the case we speak of a *false fruit*. Thus, in the Strawberry (Fig. 162 D) the true fruit consists of a number of minute achenes (*a*), but these are carried up on the much enlarged and fleshy receptacle (*r*) which constitutes the actual edible part. In the Apple (Fig. 162 E) and Pear the flesh is formed by the receptacle (*r*) in which the inferior ovary is embedded, the latter comprising what is commonly known as the core (*ov.*). The hip of the Rose (Fig. 162 C) is another false fruit in which the coloured flask-shaped envelope arises from the deeply hollowed thalamus (*r*), whilst the fruit proper is constituted by the contained achenes (*a*).

The fruits of the Mulberry and Fig differ from all those hitherto considered in being formed from complete inflorescences. In the Mulberry (Fig. 162 A) the individual units consist of achenes covered in by four perianth-members (*p*) which have become fleshy. The fruit of the Fig (Fig. 162 B) originates from a peculiar inflorescence in which the fleshy axis (*a.i.*) is deeply hollowed out, the cavity being lined with numerous minute flowers.

Many young fruits are protected by the persistent calyx (*e.g.* in Caryophyllaceæ and Labiatæ, Fig. 160 D; Mallow, Fig. 160 C; Snapdragon, Fig. 159, *e*), whilst in Compositæ the same function is fulfilled by the involucre (p. 229). In mature fruits, which have dehisced, the seeds are often shielded during wet weather by a more or less marked closing of the

valves; thus, in the Caryophyllaceæ the teeth at the top of the capsule (Fig. 159, *f*) come together under such circumstances, a feature due to unequal absorption of moisture by their two sides.

Far more important than an enumeration of the characters of fruits is the relation which these bear to the *dispersal* of the seeds. Nearly all plants produce far more seeds than can ultimately survive, the bulk of the seedlings being killed

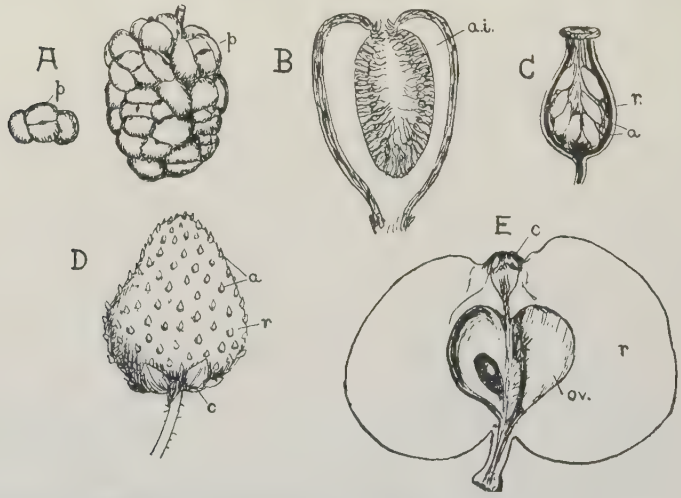


FIG. 162.—Examples of false fruits (slightly reduced). A, Mulberry; single fruit shown on left. B, Fig, in longitudinal section. *a.i.*, axis of inflorescence. C, Hip of Rose, in longitudinal section. D, Strawberry. E, Apple, in longitudinal section. *a*, achenes; *c*, calyx; *ov.*, ovary; *p*, perianth-member (in A); *r*, receptacle.

off as the result of competition with more successful ones. Since, however, plants of the same kind require similar food and conditions of growth, the struggle will be keenest between individuals of the same species; this can be observed in any seed-bed that has been too densely planted, whereas one sown with mixed seed will support a considerably greater number of individuals. Moreover, a large proportion of the seeds shed by a plant will be carried to situations unsuitable for a further development, *i.e.* they will not germinate. In view of this

great mortality it is of advantage that a plant should produce numerous seeds and that these should be widely scattered, since in this way some are certain to find a suitable situation and the risk of competition with the parent or with one another is overcome. Most plants, in fact, utilise wind or animals [1] for the better dispersal of their seeds or fruits.

A very simple type of mechanism for *wind-dispersal* consists in the production of minute and light seeds (*e.g.* Foxglove), an extreme case being seen in the Orchids in which they form a powdery mass, like pollen. Many other plants, however, propagate by light seeds of small size, which are capable of being carried considerable distances by the wind. In most of these cases the fruits are attached to the plant in such a way that the seeds are readily shaken out of them. Thus, in the Harebell the hanging fruits are disturbed by every breeze (censer-mechanism) and, in their oscillations, the seeds are gradually shaken out from the pores of the capsule (cf. above). In many Caryophyllaceæ, the Snapdragon, and the Poppy (Fig. 159, *e*, *f*, *h*), the ripe fruits are borne at the ends of stiff upright elastic peduncles which bend with sudden gusts of wind and then spring back to their normal position, thus shooting out some of the seeds like a catapult.

In a number of plants (*e.g.* Gorse, Tare, Touch-me-not) the different layers of the pericarp dry up to an unequal extent during ripening, so that a tension is created which leads, at the slightest touch, to a sudden explosive opening of the fruit, the seeds being projected some little distance. The same feature is the cause of the twisting of the fruit-valves of many members of the Leguminosæ (Fig. 159, *c*).

An expansion of the pericarp in the shape of a *wing* often helps in the distribution of one-seeded fruits, good instances being afforded by the Ash (Fig. 163 A) and the Elm. Similarly, in the Sycamore (Fig. 163 B), Maple, and many Umbelliferæ the schizocarpic fruit splits at maturity into two winged achenes. Each group of fruits in the Lime (Fig. 163 C) is suspended from the middle of a strap-shaped bract (*br.*) which not only serves as a roof, to protect the flowers and young fruits from rain, but also aids in dispersal. A similar co-operation of bracts in fruit-distribution is seen in the Horn-

[1] Regarding dispersal by water, see p. 339.

beam. Winged seeds are rarer in the British flora, but are found, for instance, in the Red Spurrey, Field Spurrey, Honesty, and Scotch Fir.

In many cases the pericarp or testa is produced into hairs, so that we obtain *plumed* fruits and seeds. Good examples of the latter are seen in the Willow and Willow-herb (Fig. 163 D),

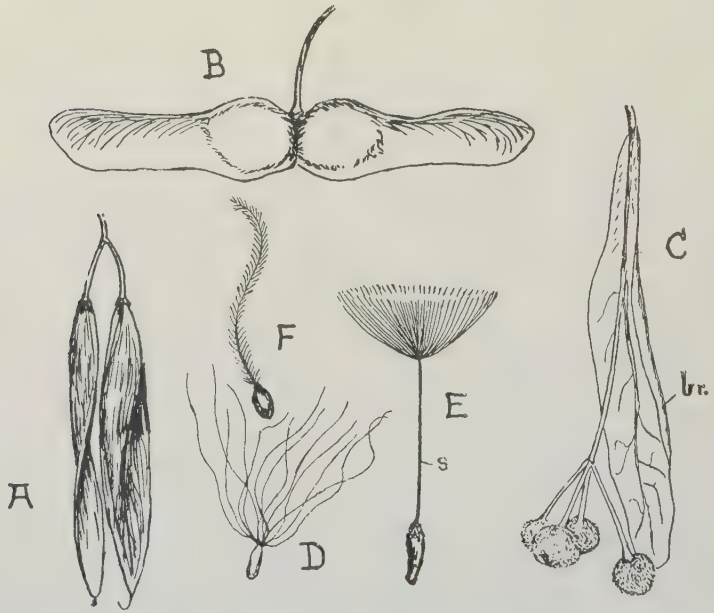


FIG. 163.—Winged and plumed fruits and seeds (all natural size). A, Ash (two winged achenes). B, Sycamore (schizocarpic, splitting into two winged achenes). C, Lime. *br.*, bract. D, Plumed seed of Willow-herb. E, Dandelion (achene with superior pappus). *s*, stalk. F, Old Man's Beard or Clematis (achene with feathery style).

both of which have capsules. In the Old Man's Beard (Fig. 163 F) and Pasque-flower the style of each achene is feathery and enlarges after fertilisation to form a plume. A peculiar type of plumed fruit is found in the Compositæ, where the calyx of the individual florets, its normal protective function being taken over by the involucre, is usually developed as a number of fine hairs (the *pappus*) arising from the top of

the inferior ovary (cf. p. 237 and Fig. 145 B and C). These hairs form a kind of parachute by means of which the achenes drift readily in the air and when, as is often the case (*e.g.* John-go-to-bed-at-noon, Field Thistle), the hairs of the pappus are themselves feathery, they are still more effective. In the Dandelion (Fig. 163 E) and John-go-to-bed-at-noon a long stalk (*s*) develops after fertilisation between the pappus proper and the ovary.

The position occupied by the pappus depends in all cases upon the amount of moisture in the air, the individual hairs spreading out more or less horizontally when the latter is dry, but closing together vertically when it is damp. Thus, the fruits only get dispersed under really favourable conditions (*i.e.* in dry air), whilst, when once on the wing, they fall to the ground with the advent of rainy weather, during which they are likely to become washed into the soil.

It has been noticed that a number of fruits have a succulent pericarp (Figs. 161, 162), amongst them being many of those which are commonly eaten. These depend for dispersal on animals and, as adaptations to this end, we can recognise the usual bright colouring, the fleshy edible character of part or whole of the pericarp, and the fact that in all these fruits the seed-contents are protected by a hard covering furnished either by the endocarp (drupes) or the testa (berries). As a consequence of the last feature, such seeds are able to pass through the digestive tracts of animals without the embryo coming to harm, the seed being deposited with the fæces; thus a certain amount of manure is available for the seedling which subsequently develops. Some of these seeds indeed will only germinate, after they have been subjected to the action of the digestive juices within the animal's body. Even when the stone is not swallowed, the bird or other animal generally carries the fruits some little distance from the parent before dropping the seeds. In the Mistletoe part of the flesh of the fruit is very sticky, so that the contained seed adheres to the bill of the bird who rubs it off on to the branch of a tree; the seedling is thus from the first attached to the plant on which it lives (p. 143).

Fleshy seeds are rare in our country, the best example being those of the Spindle-tree, in which each seed of the four

compartments of the fruit (Fig. 164 A) is enveloped by a bright orange puckered envelope (the *aril*, Fig. 164 B and C) which develops only after fertilisation and is very conspicuous when the capsule dehisces. The naked seeds of the Yew (Fig. 164 D and E) are likewise enclosed in a bright red cup-shaped aril formed during ripening. In these two forms the seeds are distributed by Birds, but in the Gorse, whose seeds have a small fleshy swelling at one end, Ants are stated to act as agents of dispersal. The

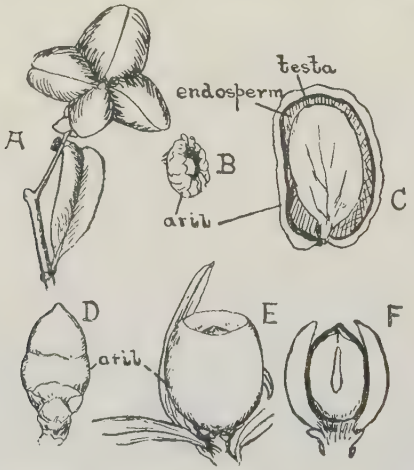


Fig. 164.—Seeds of the Spindle-tree and Yew (C considerably enlarged, other figures natural size). A–C, Spindle-tree. A, Single fruit. B, Young seed with aril. C, Ripe seed in longitudinal section. D–F, Yew. D, Young seed. E, Older seed. F, Ditto in longitudinal section.

caruncle (p. 30 and Fig. 15 A) of the Castor Oil seed is also of the nature of an aril.

A considerable number of low-growing herbs develop hooks on their fruits or on adjacent parts of the flower, and such *burr-fruits* are usually distributed by hairy animals. Thus, in the Cleavers and Enchanter's Nightshade (Fig. 165 B) the hooks are borne on the fruits themselves, whilst in Herb Bennett (Fig. 165 D) a portion of the style of each achene forms a long stiff claw. On the other hand, in the Burr Marigold (Fig. 165 C) it is the calyx that is modified, the customary pappus being here replaced by two or three stiff bristles

with backwardly directed barbs. The top part of the receptacle of the Agrimony (Fig. 165 A), again, is beset with numerous hooks, whilst in the Burdock the involucre is similarly equipped.

We have already on p. 24 described the way in which fruits and seeds get buried in the soil, but one instance deserves special consideration. In the Stork's Bill the segments of the style, which separate with the indehiscent achenes of the

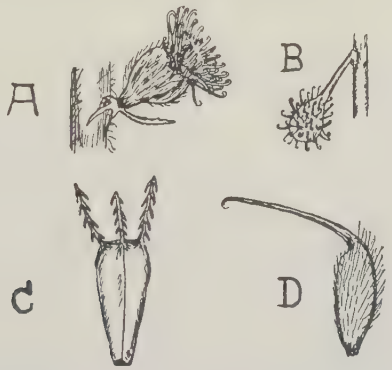


Fig. 165.—Types of burr-fruits (A and B natural size, C and D somewhat enlarged). A, Agrimony (hooks on receptacle). B, Enchanter's Nightshade (hooked fruit). C, Burr Marigold (hooked calyx). D, Herb Bennett (hooked style).

schizocarpic fruit (in the same way as in the Crane's Bill, Fig. 160 B), coil up when dry, but uncoil when moist; a similar behaviour is shown by the awns (p. 306 and Fig. 178 A, *a*), on the fruits of the Oat. Since the hairy or rough surface of the awn causes it to cling to the soil, its extension, when the latter is damp and consequently soft, results in the fruit's being driven into the ground.

CHAPTER XXIII

The Commoner Families of British Flowering Plants

Now that we have become acquainted with all the different parts of the Flowering Plant, we may proceed to consider how these plants are grouped. Such a classification is necessary in order to provide an oversight of the immense diversity of forms ; and moreover, since plants are classed on the basis of all their characteristics, classification aims at placing similar plants near together and dissimilar ones more or less far apart, so that it affords an expression of the relationships between the different forms. We therefore group plants into various aggregates resembling one another in an increasingly greater number of features.

Thus, certain forms are classed together as *species* (*e.g.* the different forms of Shepherd's-purse, cf. Fig. 3), the individuals differing only in minute details, such as shape of leaves, presence or absence of hairs, time of flowering, etc. Different species are grouped together in a wider aggregate, the *genus*, as for example the diverse kinds of Buttercups ; all the species of such a genus resemble one another in certain important characters, but differ in more numerous and more appreciable respects than the individuals of the same species. For instance, in the case of the Buttercups, all the species agree in having flowers with a calyx and corolla, nectary-bearing petals, numerous stamens, a fruit composed of a collection of achenes, etc. The individual species, on the other hand, differ in habit, in the shape and degree of lobing of the leaves, the size and colour of the petals, the form of the peduncle, and the character of the pericarp, as well as in many other small points. The Buttercups, together with other genera such as the Clematis, Anemone, Marsh Marigold, Christmas Rose, Columbine. Monks-

hood, Larkspur, etc., are comprised in the *family* or *natural order* Ranunculaceæ, all of them being distinguished by possessing leaves with sheathing bases, a hypogynous flower, numerous stamens, an apocarpous ovary, and fruits usually consisting of achenes or follicles. On the whole, floral characters are of greater importance in distinguishing genera than the vegetative organs which serve more particularly to identify species, since the features of the flower are more constant among related forms.

All the species of a given genus are in scientific usage designated by a common Latin name, all the Buttercups, for instance, being described as species of the genus *Ranunculus*. The species are distinguished by a second Latin word placed after that denoting the genus; thus, the Meadow Buttercup is known as *Ranunculus acris*, whilst the Field Buttercup is *Ranunculus arvensis*. In the following summary of families the Latin name of each genus is placed in brackets after it.

We have frequently referred to the two great groups of Flowering Plants, the Monocotyledons and Dicotyledons. These have been seen to be distinguished from one another in the main by (i) the structure of the embryo (pp. 34, 36), (ii) the shape and venation of the leaves (pp. 86, 88), (iii) the arrangement of the vascular strands in the stem (p. 99), and (iv) the structure of the flower (pp. 233, 235). We will now enumerate the characters of some of the more important British families belonging to each group, special features of interest being mentioned in the case of most genera.

A. DICOTYLEDONS[1]

(*a*) POLYPETALOUS AND APETALOUS FAMILIES

1. Salicaceæ

Trees and shrubs with alt. stip. leaves, the stipules often caducous (p. 93); suckers (p. 154) frequently produced. Infl. a catkin

[1] In describing the following families we shall frequently employ a *floral formula* to indicate the usual number of parts in the successive whorls. The number of members in each is represented by a numeral and, where there is more than one whorl of the same kind, the numbers for each are joined by a + sign. The calyx is represented by K, the corolla by C, a perianth by P, the stamens by A, and the ovary by G. The joining together of members of a whorl is indicated by putting the corresponding numeral in brackets, whilst a line above or below the numeral

(p. 228) with large hairy bracts. Flrs. diœcious (p. 253), unisex., hypog., naked. ♂ flrs. (Fig. 166 ♂) with 2–∞ sta., having often brightly coloured anthers. ♀ flrs. (Fig. 166 ♀) with a sup., bicarpellary, unilocular ov. with two parietal placs. bearing ∞ ovules; stigma bilobed. Small nectary (Fig. 166, *gl.*) in both flrs. Fruit a capsule; seeds exalb. bearing tufts of hairs. Entom. or anem.

The British forms are:—Willow (Fig. 166), Sallow, Osier (*Salix*), with 2–5 sta. in the ♂ flrs., usually narrow leaves, and a one- or two-toothed nectary; Poplar, Aspen (*Populus*), with ∞ sta., broad leaves, and a cup-shaped structure analogous to the nectary of *Salix*. The latter is entom., *Populus* anem.

The Hazel (*Corylus*) (Fig. 129) belongs to a closely allied family.

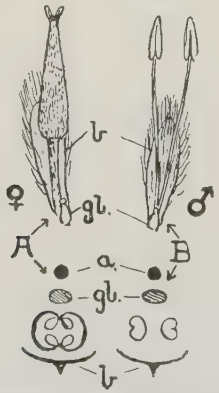


Fig. 166.—Structure of flowers of Goat Willow (enlarged). The ♂ and ♀ flowers above and the corresponding floral diagrams below. *a*, axis of catkin; *b*, bracts; *gl.*, honey-glands.

2. Ranunculaceæ

Mostly perennial herbs with alt. (except Clematis), occasionally stip. leaves, often deeply palmately lobed and having sheathing

representing the ovary marks the inferior or superior position of the latter. Apart from this, the following abbreviations are employed: *alb.*, albuminous; *alt.*, alternate; *anem.*, anemophilous; *apocarp.*, apocarpous; C, corolla; *cpd.*, compound; *cpl.*, carpel; *entom.*, entomophilous; *epig.*, epigynous; *exalb.*, exalbuminous; *exstip.*, exstipulate; *flr.*, flower; *hypog.*, hypogynous; *inf.*, inferior; *infl.*, inflorescence; *irreg.*, irregular; K, calyx; *opp.*, opposite; *ov.*, ovary; *perig.*, perigynous; *plac.*, placenta; *protandr.*, protandrous; *protog.*, protogynous; *reg.*, regular; *sp.*, species; *sta.*, stamen; *stip.*, stipulate; *sup.*, superior; *syncarp.*, syncarpous; *unisex.*, unisexual; ♂, male; ♀, female; ☿, hermaphrodite; ∞, numerous.

bases; stem a root-stock (p. 156) with fibrous roots and often bearing radical leaves. Infl. usually cymose, but sometimes a raceme (Larkspur, Monkshood) or a single terminal flr. (Anemone). Flrs. mostly reg. (irreg. in Larkspur, Monkshood), ☿, hypog., all parts free, commonly with A∞ G∞ (Fig. 167). Perianth either consists of K and C (Buttercup, Fig. 132 A) or of one or more petaloid (*i.e.* coloured) whorls; sta. ∞, often extrorse, mostly spiral; ov. apocarp., sup. Nectaries of various shapes, between sta. and perianth. Fruit a collection of achenes or follicles (capsule in Love-in-a-Mist, berry in Baneberry); seeds alb. Mostly entom. and often protandr. An acrid juice (sometimes poisonous) often present.

The family is subdivided into *Anemoneæ* (with achenes) and *Helleboreæ* (with follicles).

The principal British genera of *Anemoneæ* are: the Anemones

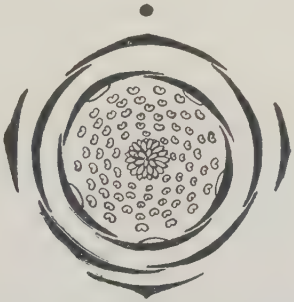


Fig. 167.—Floral diagram of Buttercup.

(*Anemone*), with an involucre of 3 bracteoles (p. 226), the Wood Anemone having a pollen-flower; the Old Man's Beard (*Clematis*), a woody climber with opp. leaves, pollen-flrs., and feathery styles (Fig. 163 F); Mouse-tail (*Myosurus*), with a much elongated receptacle (p. 232) and few sta.; the Buttercups (*Ranunculus*, Fig. 167), with a number of aquatic sp. (Water Crowfoots, Fig. 199), usually with white flrs. and membranous stipules; Meadow-rue (*Thalictrum*), with stip. leaves, a small deciduous perianth, and with pollen-flowers or anem.

The British members of the *Helleboreæ* are: Monkshood (*Aconitum*), with irreg. flrs. and reduced petals, two of which form nectaries beneath the hood (Fig. 154); Baneberry (*Actæa*), with a berry formed from only 1 cpl.; Columbine (*Aquilegia*), with 2 perianth-whorls, each of the inner members being produced into a honey-forming spur; Marsh Marigold (*Caltha*), marsh-plant with cordate leaves and honey at base of cpls.; Larkspur (*Delphinium*), irreg. flr. having a single spur into which two nectary-bearing pro-

cesses from the petals project (p. 257); Winter Aconite (*Eranthis*), Fig. 142, with a leafy involucre just below flr. and small tubular nectaries; Hellebore and Christmas Rose (*Helleborus*), with a persistent perianth-whorl, often green, and trumpet-shaped nectaries (Fig. 146 D); Love-in-a-Mist (*Nigella*), cultivated, with an involucre of bracteoles just beneath flr., tubular nectaries, syncarp. ov., and capsular fruit; Globe-flower (*Trollius*), with perianth completely covering flr. which is usually self-pollinated.

3. Caryophyllaceæ

Annual or perennial herbs with opp., often exstip., entire leaves and swollen nodes, mostly glabrous (p. 87). Infl. mostly a dichasial cyme (Fig. 130 B). Flrs. reg., mostly ☿ (sometimes unisex. in Campion), hypog., usually with K5 C5 A5+5 G(3 to 5). K poly- or gamosepalous; petals free, often divided or clawed, sometimes

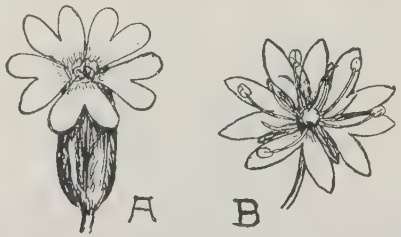


Fig. 168.—A, Flower of Campion, showing gamosepalous calyx. B, Flower of Stitchwort, showing deeply cut petals and open type of flower (B enlarged).

with a corona (Campion), or absent; sta. in 2 whorls, mostly 10, sometimes 8, often of two lengths; ov. sup., syncarp., of 3–5 cpls., either opp. the petals or sepals, with a free central plac., usually bearing ∞ ovules. Stigma with as many lobes as there are cpls. Honey formed at base of sta. (Fig. 146 C). Fruit usually a capsule opening by apical teeth (Fig. 159, *f*), an achene in the Knawel; seeds alb., with embryo towards outside and sculptured testa. Mostly entom., commonly protandr. Non-poisonous.

The family is subdivided into:—

(i) *Alsineæ*:—Calyx polysepalous; flrs. open and shallow (Fig. 168 B). The British genera are: Sandwort (*Arenaria*), with the Sea-Purslane, a maritime sp.; Mouse-ear Chickweed (*Cerastium*), with notched petals and hairy leaves; Pearl-wort (*Sagina*), some sp. being apetalous and self-pollinated; Knawel (*Scleranthus*), with stipules, flrs. apetalous and self-pollinated, with only 1 ovule, fruit an achene, a common weed of cornfields;

Field Spurrey (*Spergula*), a weed with stip. and dwarf-shoots (Fig. 42); Sandwort Spurrey (*Spergularia*), maritime, with stip. leaves; Stitchwort and Chickweed (*Stellaria*), with deeply split petals (Fig. 168 B); the Chickweed flrs. all the year round, although in winter the flrs. are often cleistogamic (p. 277).

(ii) *Sileneæ*:—Calyx gamosepalous; petals clawed; tubular flrs. (Fig. 168 A). The British forms are: Pink (*Dianthus*), with fringed petals (Fig. 136 A) and only 2 styles; Corn-cockle (*Githago*), a common weed of cornfields, with long-toothed sepals and entire petals; Campion (*Lychnis*), Fig. 168 A, with a well-marked corona (p. 239); Bladder Campion or Catch-fly (*Silene*), often with an inflated K. The last two genera are often Butterfly- or Moth-pollinated (p. 274).

4. Cruciferæ

Annual or perennial herbs with alt., exstip. leaves, often bearing branched hairs; leaves simple or more or less pinnately lobed (Fig. 3), often radical; roots occasionally tuberous. Infl. a raceme without bracts, often corymbose at first (p. 227). Flrs. usually white or yellow, reg., ♀, hypog., all parts except cpls. free, usually with K2+2 C4 A2+4 G(2) (Fig. 169). Calyx of 2 outer median and 2 inner lateral sepals, often upright; petals often clawed and alternating with the 4 sepals; sta. 2 short lateral and 4 long median ones (tetradynamous, p. 242); ov. syncarp., bicarp., with a false septum (p. 247) and 2 parietal placs., sup. Stigma usually bilobed. Nectaries at base of 2 short sta., the honey collecting in pouches formed by the lateral sepals (p. 257 and Fig. 147). Fruit a siliqua (Fig. 159, *d*) or silicula (Fig. 4 B); seeds exalb., with a curved embryo. Mostly entom. and protandr. Non-poisonous.

Fig. 169.—Floral diagram of Cruciferæ (Wallflower).

The following British genera have siliquas: Rock-cress (*Arabis*), to which genus belongs the Mountain Snow; Winter-cress (*Barbarea*), occasionally with bracts to infl.; Charlock

(*Brassica*), including Cabbage, Cauliflower, Kohl-rabi, Mustard, Turnip, Brussels Sprouts; Milkmaid (*Cardamine*), fond of marshy situations and often having explosive fruits (p. 285); Wallflower (*Cheiranthus*), Fig. 147; Coral-root (*Dentaria*), with bulbils (p. 165); Stock (*Matthiola*), a maritime plant with a very hairy shoot; Water-cress (*Nasturtium*); Jack-by-the-hedge or Hedge Mustard (*Sisymbrium*), with leaves tasting of garlic.

The following have siliculas: Shepherd's-purse (*Capsella*), a weed; Scurvy Grass (*Cochlearia*), maritime, often with succulent leaves, the Horse-radish being a sp. of this genus; Whitlow-grass (*Draba*); Candytuft (*Iberis*), with a very typical corymb (Fig. 146*) having enlarged marginal flrs.; Cress (*Lepidium*), with slimy seeds (p. 43); Awlwort (*Subularia*), a submerged aquatic with cylindrical leaves.

In the following genera the fruits are indehiscent, being either one-seeded or breaking up into one-seeded portions: Sea-rocket (*Cakile*), maritime, with fleshy leaves; Sea-kale (*Crambe*), maritime, with fleshy leaves and a spherical fruit; Woad (*Isatis*), employed in dyeing; Radish (*Raphanus*), with a constricted siliqua breaking up into one-seeded segments; Wart-cress (*Senebiera*), a common weed with two-seeded fruits.

5. Rosaceæ

Perennial herbs (except the Field Lady's Mantle which is an annual), shrubs, or trees, with alt., often stip. leaves which are simple or compound. Infl. cymose or racemose. Flrs. reg., mostly ☿, hypog. or epig. or most commonly perig., all parts generally free, usually with K5 C5 A5+5+5+ . . . G∞. Calyx occasionally with an epicalyx (p. 238, Strawberry, Cinquefoil); sta. in several whorls of 5, although few in certain genera; ov. usually apocarp. and sup. (syncarp. and inf. in Apple, Pear, etc.). Receptacle more or less hollowed out (Fig. 131 B–E). Honey formed on receptacle between sta. and cpls. Fruit various, a drupe or an aggregate of drupes or achenes; false fruits (Fig. 162 C–E) in certain genera. Mostly entom. and often protandr.

The following subdivisions of the family are British:—

(i) *Spiræoideæ*:—Relatively few whorled cpls. borne on a small central protuberance of the but slightly concave receptacle (Fig. 131 B); fruit a number of achenes. The commonest British representative is the Meadow-sweet (*Spiræa*), a marsh-plant with twisted cpls.

(ii) *Pomoideæ*:—Shrubs or trees, with an inf. syncarp. ov.; generally a false fruit. There are two British genera. Hawthorn (*Cratægus*), with stem-spines (p. 180); and Apple, Pear, Medlar, and Mountain Ash (*Pyrus*).

(iii) *Rosoideæ*:—Shrubs and herbs, with apocarp., perig. flrs. and a more or less deeply hollowed receptacle (Fig. 131 C and D). The most important forms are: Agrimony (*Agrimonia*), with cup-shaped receptacle bearing hooks in fruiting stage (Fig. 165 A), ov. of 1 or 2 cpls.; Lady's Mantle (*Alchemilla*), apetalous tetramerous flrs., with cup-shaped receptacle, few cpls., Fly-pollinated; Strawberry (*Fragaria*), with runners (Fig. 85), an epicalyx, false fruit (Fig. 162 D); Herb Bennett or Avens (*Geum*), with epicalyx (Fig. 135 D) and concave receptacle like *Fragaria*, fruit of hooked achenes (Fig. 165 D); Cinquefoil, Tormentil (*Potentilla*), often with runners (p. 153), an epicalyx, concave receptacle, fruit a number of achenes; Salad Burnet (*Poterium*), apetalous unisex. tetramerous flrs. with branched stigmas, fruit of 1–3 achenes, anem.; Rose (*Rosa*), a scrambler (p. 20), with a false fruit largely composed of the deeply hollowed receptacle (Fig. 162 C); Blackberry, Raspberry, Bramble (*Rubus*), scramblers, with fruit consisting of a number of drupes (Fig. 161 G and H).

(iv) *Prunoideæ*:—Trees, with a single cpl. in a concave receptacle. Fruit a drupe (Fig. 161 E and F). The British forms are Almond, Apricot, Cherry, Plum, Sloe (*Prunus*), frequently with extrafloral nectaries (p. 257) at base of leaf.

6. Leguminosæ

Annual or perennial herbs, shrubs, or trees, with alt. stip. leaves, usually cpd. and pinnate, leaflets entire and often mucronate (p. 87 and Fig. 46 H), frequently modified into tendrils (p. 216); roots with root-tubercles (p. 147 and Fig. 80). Infl. racemose. Flrs. irreg., ☿, slightly perig., usually with K(5) C5 A(5+5) G1 (Fig. 170). K more or less gamosepalous, frequently two-lipped (Fig. 150 A), odd sepal anterior (Fig. 170); C papilionaceous (cf. p. 263), petals free, consisting of posterior standard, 2 lateral wings, and 2 slightly joined anterior petals forming the keel which encloses the essential organs; sta. joined by their filaments to form a tube (Fig. 170), or one only (the posterior one) free (Fig. 133 C); ov. sup., monocarp., usually pod-like, enclosed in sta.-tube, with ovules parietal on ventral suture. Honey formed by bases of sta., only in those forms with a free sta. Fruit a legume (Fig. 159 C). All entom., visited mainly by Bees. Many are common meadow-plants.

The commoner genera which all belong to the subdivision *Papilionaceæ* are: Kidney-vetch (*Anthyllis*), with inflated hairy calyx; Broom, Laburnum (*Cytisus*), the Broom a switch-plant (p. 175), all 10 sta. joined, pollen-flrs. (Fig. 150 A and B); Petty Whin, Needle Furze (*Genista*), all 10 sta. joined, pollen-flrs.; Everlasting Pea, Sweet-pea (*Lathyrus*), Fig. 150 C–E, with terminal part of

leaf modified to tendrils, large stips., and winged stems and petioles (Figs. 123 B and 47 D); Bird's-foot Trefoil (*Lotus*), Fig. 151, with piston-mechanism; Medick (*Medicago*), with heads of small flrs. and spirally coiled legumes, frequently provided with hooks for animal-distribution, often indehiscent; Melilot (*Melilotus*), with keel-petals free from one another; Rest-harrow (*Ononis*), a plant with stem-spines, all 10 sta. joined; Runner Bean (*Phaseolus*); Pea (*Pisum*); Clover (*Trifolium*), with flrs. in racemose heads (Fig. 149) and trifoliate leaves; Furze or Gorse (*Ulex*), a spiny plant (Fig. 99 D) characteristic of heaths and commons, with explosive fruits (p. 285), all 10 sta. joined, flrs. like those of *Cytisus*; Tare or Vetch, Broad Bean (*Vicia*), with pinnate leaves often ending in tendrils.

In the following forms the legume is indehiscent (*i.e.* a so-called *lomentum*), breaking up at maturity into a number of one-seeded parts: Horseshoe-vetch (*Hippocrepis*); Sainfoin (*Onobrychis*); Bird's-foot (*Ornithopus*).

Fig. 170.—Floral diagram of Leguminosæ (Needle Furze).

Amongst foreign forms, commonly seen in this country, some have papilionaceous flrs. with 10 free sta. (*e.g.* Judas tree), whilst others have reg. flrs. which are densely grouped (*Mimosa*) or have ∞ conspicuous sta. (*Acacia*).

7. Umbelliferæ

Mostly perennial herbs, with large, alt., exstip., usually cpd. leaves having big sheathing bases (Fig. 47 C); stem hollow and often ribbed (Fig. 53 A); a prominent tap-root generally present. Infl. usually a cpd. umbel (p. 228), frequently with enlargement of the petals of the outermost flrs. (p. 258). Flrs. small, usually white or yellow, reg., ☿, epig., all parts except cpls. free, almost invariably with K5 C5 A5 G(2) (Fig. 171). K very small and inconspicuous; petals often distant from one another; sta. 5, introrse; ov. inf., biloc., with 1 ovule in each compartment; stigma bilobed. Nectary as a disc on top of ov. (Fig. 146 E). Fruit a schizocarp (Fig. 160 A);

seeds alb. Mostly protandr. and visited by Flies. All parts of the plant usually contain aromatic oils, often of commercial value (*e.g.* Angelica, Aniseed, Caraway, etc.).

The following are some of the commoner British forms: Bishop's-weed (*Aegopodium*); *Angelica*, used as a sweetmeat; Beaked Parsley (*Anthriscus*), a hedge-plant flowering very early in the spring; Caraway, Parsley (*Carum*); Pig-nut (*Conopodium*), with a tuberous root-stock, common in woods and meadows; Rock-samphire (*Crithmum*), found on rocky coasts, with fleshy leaves, employed as a pickle; Carrot (*Daucus*), with a tuberous root (Fig. 30 A) and spiny fruits; Sea-holly (*Eryngium*), a sand-dune plant, with palmately lobed spinous leaves and cymose capitula (p. 230) of blue flrs.; Fennel (*Fœniculum*), used in flavouring; Hogweed (*Heracleum*), a hedge-plant with huge umbels; Marsh Pennywort (*Hydrocotyle*), with peltate leaves; Water Dropwort (*Oenanthe*), a marsh- or water-plant with swollen stems; Parsnip

Fig. 171.—Floral diagram of Umbelliferæ (Hogweed).

(*Peucedanum*), with a tuberous root, the wild form characteristic of chalk-pastures; Wood Sanicle (*Sanicula*), with flrs. in cymose umbels, simple palmately lobed leaves, and fruits with hooked spines; Shepherd's Needle or Venus' Comb (*Scandix*), a common weed of cultivated ground, with much elongated fruits.

The following are very poisonous: Fool's Parsley (*Aethusa*), a garden-weed; Wild Celery (*Apium*), the form used commercially having been rendered harmless by cultivation; Water Hemlock (*Cicuta*), a marsh-plant; Hemlock (*Conium*).

(*b*) GAMOPETALOUS FAMILIES

1. Primulaceæ

Annual or perennial herbs, with generally simple, alt., exstip. leaves, often radical. Infl. racemose, a raceme or umbel, or with solitary flrs. Flrs. reg., ☿, hypog., pentamerous, usually with K(5)

C(5) A5 G(5) (Fig. 172). K mostly gamosepalous ; C gamopetalous (but deeply cleft and almost polypetalous in the Pimpernel and the Loosestrife), often with a long corolla-tube (Fig. 148) ; sta. 5, opp. the petals and epipetalous (p. 244) ; ov. sup. (except the Brookweed), uniloc., with free central plac. bearing ∞ ovules (Fig. 148) ; stigma capitate (p. 246). Honey often formed at base of ovary. Fruit a capsule opening by teeth (except Scarlet Pimpernel and Bastard Pimpernel, where there is a lid) ; seeds alb. Mostly entom., occasionally showing heterostyly (p. 262).

The British genera are : Scarlet Pimpernel (*Anagallis*), a common weed of cornfields, with hairy filaments and small stalked glands on petals ; Bastard Pimpernel (*Centunculus*), a minute plant found in wet places ; Sowbread (*Cyclamen*), with cordate leaves, tuberous root-stock, petals turned back, and a short corolla-tube ; Sea Milkwort (*Glaux*), a succulent maritime plant, apetalous, self-pollinated ; Water-Violet (*Hottonia*), heterostylic ; Creeping

Fig. 172.—Floral diagram of Primulaceæ (Primrose).

Jenny, Yellow Pimpernel, Loosestrife (*Lysimachia*), some sp. heterostylic, others with teeth (staminodes, p. 243) alt. with the sta. ; Cowslip, Oxlip, Primrose (*Primula*), Fig. 148, with heterostylic flrs. ; Brookweed (*Samolus*), a marsh-plant, with staminodes (p. 243) alt. with the sta., ovary partly embedded in the receptacle, and bracts borne half-way up the peduncles ; Winter-green (*Trientalis*), subalpine plant somewhat resembling a Wood Anemone.

2. Labiatæ

Annual or perennial herbs, with opp., exstip., often hairy leaves ; square hollow stems (Figs 43 C and 53 B), swollen at the nodes. Infl. cpd., primarily racemose, but axillary flr.-clusters are dichasia (cf. p. 230). Flrs. irreg., ☿ (but occasionally unisex.), hypog., usually with K(5) C(5) A4 G(2) (Fig. 173). K gamosepalous, generally with 5 prominent teeth, often slightly irreg. (Fig. 135 C) ; C bilabiate (Fig. 137 D), gamopetalous, often with hairs at mouth of corolla-tube ; sta. 4, didynamous (p. 242), beneath hood-like

upper lip of corolla (p. 267) ; ov. sup. bicarp., but quadriloc. owing to false septum (p. 247), each loculus with 1 ovule ; stigma bilobed. Honey produced by a disc round base of ov., or restricted to its anterior side. Fruit schizocarpic of 4 achenes (Fig. 160 D), protected by persistent K ; seeds exalb. All entom. and mostly protandr. Leaves often with glandular hairs (p. 182) forming aromatic oils (*e.g.* Lavender, Rosemary, Marjoram).

The commonest British genera are : Bugle (*Ajuga*), a woodland-plant with a small upper lip ; Black Horehound (*Ballota*) ; Calamint (*Calamintha*), a common hedge-plant ; Hemp-nettle (*Galeopsis*) ; Dead-nettle (*Lamium*), common weeds ; Horehound (*Marrubium*), a plant with a bitter taste ; Mint (*Mentha*), aromatic herbs, frequently found in marshes ; Ground Ivy (*Nepeta*), Fig. 8 ; Self-heal (*Prunella*), a meadow-plant ; Skull-cap (*Scutellaria*), a marsh-plant, with two-lipped calyx, the upper lip bearing a pouch-like outgrowth ; Woundwort (*Stachys*), to this genus belongs the Chinese

Fig. 173.—Floral diagram of Labiatæ (Dead-nettle).

Artichoke ; Wood-sage (*Teucrium*), found on dry heaths and in woods, with a very small upper lip ; Thyme (*Thymus*), on heaths, aromatic, with an almost reg. corolla.

The following have only 2 (anterior) perfect sta. : Gipsy-wort (*Lycopus*), a marsh-plant, with 2 perfect and 2 imperfect (posterior) sta. ; Sage (*Salvia*), with an interesting pollination-mechanism (p. 268 and Fig. 152).

3. Scrophulariaceæ

Annual or perennial herbs, with alt. or opp., exstip., often hairy leaves, frequently with square stems. Infl. racemose or cymose. Flrs. usually irreg., ☿, hypog., generally with K(5) C(5) A4 G(2) (Fig. 174 C). K gamosepalous, mostly irreg. ; C various ; sta. usually 4, didynamous (p. 242) ; ov. sup., bicarp., biloc., with swollen axile placs. bearing ∞ ovules (Fig. 153 D) ; stigma bilobed. Honey formed in a disc beneath the ov. Fruit a capsule ; seeds alb. All entom., mostly protandr. Many poisonous.

The principal British genera are: Snapdragon (*Antirrhinum*), Fig. 153, with a personate (p. 237) corolla; Foxglove (*Digitalis*), a woodland-plant, with alt. leaves and irreg. tubular corolla (Fig. 137 E), poisonous; Toothwort (*Lathræa*, Frontispiece), a parasite; Toadflax (*Linaria*), with a personate corolla and a spur acting as a honey-bag (p. 257); Musk (*Mimulus*), a river-side plant, with stigma sensitive to touch (p. 221 and Fig. 125); Figwort (*Scrophularia*), hedge- or marsh-plants, with posterior staminode and markedly protog. flrs. (Figs. 140 and 174 C); Mulleins (*Verbascum*), mostly hedge-plants, with alt. leaves, 5 sta. with very hairy filaments, and almost reg. flrs. (Fig. 174 A); Speedwells (*Veronica*), with almost reg. flrs. having K4 C4 (posterior petal larger than the others) A2 G(2) (Fig. 174 B).

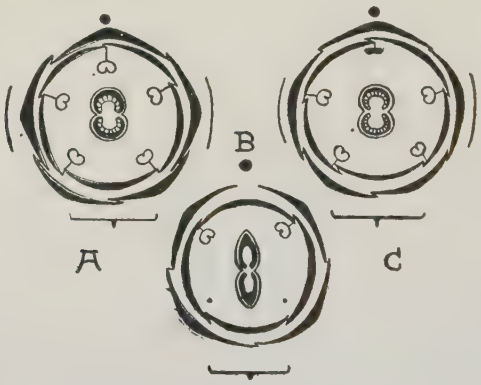


FIG. 174.—Floral diagrams of Scrophulariaceæ. A, Mullein. B, Speedwell. C, Figwort.

The following are all meadow-plants and semi-parasites (p. 139): Red Eye-bright (*Bartsia*), Fig. 73; Eye-bright (*Euphrasia*); Cow-wheat (*Melampyrum*); Red Rattles or Louseworts (*Pedicularis*); Yellow Rattle (*Rhinanthus*).

4. COMPOSITÆ

Annual or perennial herbs, with usually alt., exstip. leaves, often hairy. Infl. a capitulum (p. 228), with an involucre of bracts, composed either of disc- and ray-florets (Fig. 145 A), or of strap-shaped florets only (Fig. 175 A), or of tubular ones only (p. 273). Flrs. rarely with bracts, frequently yellow, reg. or irreg., ☿ or unisex., epig., usually with Ko C(5) A(5) G(2) (Fig. 175 C). K usually absent or represented by a pappus (p. 286); C gamopetalous,

petals joined to form a tube or a strap-shaped structure (Figs. 135 E, 137 F, and 175 A); sta. syngenesious (p. 244), introrse; ov. inf., uniloc., bicarp., with 1 basal ovule; stigma bilobed. Nectary ring-shaped round base of style. Fruit an achene, with pericarp and testa joined (p. 279), surmounted by the pappus (p. 286). Mostly entom. and protandr. (cf. p. 273). A considerable number are common weeds.

The family is subdivided into:—

(i) *Tubuliflorœ*:—Disc-florets tubular; no latex. The chief British forms are: Milfoil (*Achillea*), meadow-weed, with few-flowered capitula densely aggregated into corymbs, and white or pink flrs.; Mayweed (*Anthemis*), cornfield-weeds, with bracts to individual flrs.; Michaelmas Daisy (*Aster*), the British form maritime with fleshy leaves; Daisy (*Bellis*), a common weed of lawns and

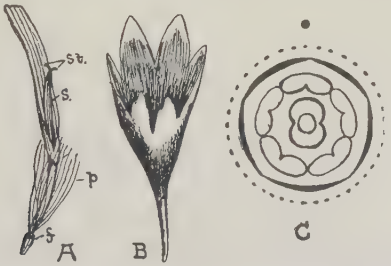


FIG. 175.—A, Strap-shaped hermaphrodite floret of Dandelion (enlarged). *f*, ovary; *p*, pappus; *s*, stamen-tube; *st.*, stigma. B, Neuter floret of Cornflower (enlarged). C, Floral diagram of hermaphrodite floret of Compositæ.

pastures; Burr Marigold (*Bidens*), marsh-plant, with fruits surmounted by barbed bristles (Fig. 165 C); Dog-daisy (*Chrysanthemum*), a meadow-plant; Fleabane (*Erigeron*), a chalk-plant; Golden Samphire, Ploughman's Spikenard, Elecampane (*Inula*); Chamomile (*Matricaria*), common cornfield-weeds; Fleabane (*Pulicaria*), a common ditch-plant; Groundsel, Ragwort (*Senecio*), common weeds; Golden Rod (*Solidago*); Coltsfoot (*Tussilago*), common weed, with solitary capitulum appearing very early, before the leaves, and having unisex. flrs. only (p. 253).

The following members of Tubuliflorœ have only tubular flrs. in their capitula: Burdock (*Arctium*), common weed, fruits distributed by hooks on involucre (p. 289); Catsfoot (*Antennaria*), on heaths, with diœcious capitula and white or pink flrs.; Mugwort, Absinth, Wormwood (*Artemisia*), maritime or hedge-plants, very hairy; Thistles (*Carduus*, *Cnicus*), with spiny leaves and

purple or white flrs., often weeds; Hardheads, Cornflower (*Centaurea*), with neuter outer flrs. (p. 259 and Fig. 175 B), irritable sta., and fringed bracts to involucre; Hemp Agrimony (*Eupatorium*), a marsh-plant with opp. leaves; Cudweed (*Filago*), with dense covering of white hairs; Tansy (*Tanacetum*), used medicinally.

(ii) *Liguliflorœ*:—All florets strap-shaped (Fig. 175 A); latex (p. 138) present. The more important British members are: Chicory (*Cichorium*), common weed with blue flrs.; Hawkweed (*Hieracium*), with very numerous sp.; Cat's-ear (*Hypochœris*), a meadow-plant with scaly bracts to individual flrs.; Lettuce (*Lactuca*); Nipplewort (*Lapsana*), common garden-weed, without a pappus; Sow-thistle (*Sonchus*), cornfield-weeds; Dandelion (*Taraxacum*), common weed with tuberous root; John-go-to-bed-at-noon, Salsify (*Tragopogon*), with tuberous root, narrow grass-like leaves, and long bracts.

The following Compositæ are often cultivated: Artichoke and Cardoon (*Cynara*), young capitula of former used as a vegetable; *Dahlia*, with tuberous roots; Sunflower, Jerusalem Artichoke (*Helianthus*); *Scorzonera*, a vegetable, with tuberous root.

B. MONOCOTYLEDONS

1. Liliaceæ

Perennial herbs, with underground rhizomes or bulbs, and sheathing lanceolate leaves, often radical. Infl. various, commonly araceme. Flrs. reg., ☿, hypog., generally with P3+3 A3+3 G(3); (Fig. 176). P generally petaloid and trimerous, free or joined sta. 6, occasionally epipetalous (p. 244); ov. sup., triloc., with axile placs., usually bearing ∞ ovules. Honey often formed in ovary-wall (p. 255). Fruit a berry or capsule; seeds alb. Many early-flowering.

The chief British forms having berries are: *Asparagus*, with linear cladodes (p. 176 and Fig. 97), the young shoots being used as a vegetable; Lily of the Valley (*Convallaria*), and Solomon's Seal (*Polygonatum*), both woodland-plants with a gamopetalous perianth, the latter with leafy stems; Herb Paris (*Paris*), woodland-plant, with an often tetramerous flr., and Fly-pollinated (p. 275); Butcher's Broom (*Ruscus*), a woodland-plant with broad leaf-like cladodes (p. 176 and Fig. 98 B) bearing unisex. flrs., the ♂ with 3 sta., the ♀ with a uniloc. ov.

The following British genera have capsules: Onion, Garlic (*Allium*), with a cymose umbel (p. 229), flrs. often replaced by bulbils (p. 165); Meadow Saffron (*Colchicum*), meadow-plant, with a corm and a very long corolla-tube, flrs. in autumn, fruits in spring when

the leaves appear; Crown Imperial (*Fritillaria*); Lily (*Lilium*), with anthers movable on tops of filaments; Grape Hyacinth (*Muscari*), with very small perianth-lobes; Bog Asphodel (*Narthecium*), marsh-plant with erect leaves; Star of Bethlehem (*Ornithogalum*); Wild Hyacinth (*Scilla*), in woods; Tulip (*Tulipa*).

2. Orchidaceæ

Perennial herbs, often with tuberous roots; roots mostly associated with a Fungus (p. 146); leaves lanceolate or scaly, often radical. Infl. racemose, often a spike and frequently with coloured bracts. Flrs. irreg., ☿, epig., twisting through half a circle during their development (cf. p. 272 and Fig. 156 B), generally with P3+3 A1 G(3) (Fig. 177). P of 2 petaloid whorls, the posterior member

Fig. 176.—Floral diagram of Liliaceæ.

(in mature flr. anterior in position) of the inner whorl enlarged to form the labellum (Fig. 156 A–C, *l*). Essential organs, borne on a central column (Fig. 156 D, *c*) and generally consisting of 1 large sta. and a tricarp. ov. Sta. at top of column, with 2 prominent anther-lobes, each occupied by a pollinium (*p* in Fig. 156 D, see also p. 273) which is attached by a short stalk-like prolongation (*ca.*) to a pouch (*r*) above the stigmatic surfaces (*s*); 2 staminodes (*Std.*) often present on either side of the fertile sta.; ov. inf., generally elongated and stalk-like (Fig. 156 B, *o*), uniloc., with 3 parietal placs. each bearing ∞ ovules; stigmatic surfaces 2, often more or less confluent. Labellum often prolonged into a spur (Fig. 156 B, *sp.*), at base of which the honey is formed. Fruit a capsule with ∞ very minute exalb. seeds (cf. p. 285). Mostly entom. Many are found in woodlands, often on chalk-soils.

The family is subdivided into *Monandræ* (with only one fertile

sta.) and *Diandræ* (with 2 fertile sta.), the former being mainly represented in Britain.

The principal British genera of *Monandræ* are: Man-Orchis (*Aceras*), with 4 pronounced lobes to labellum, no spur, green flrs.; Coral-root (*Coralliorhiza*), a saprophyte (p. 143); Helleborine (*Epipactis*), greenish-purple flrs., Wasp-pollinated; Butterfly-Orchis (*Habenaria*), Moth-pollinated, with night-scented white flrs., (p. 274) and long spurs containing free honey; Twayblade (*Listera*), with 2 prominent leaves and greenish flrs.; Bird's-nest Orchid (*Neottia*), Fig. 77, a saprophyte (p. 143) with brownish flrs.; Bee-Orchis, Fly-Orchis (*Ophrys*), flrs. without a spur and resembling various insects; *Orchis* (Fig. 156); Lady's Tresses (*Spiranthes*), with a twisted spike and fragrant white flrs.

The only member of *Diandræ* in Britain is the Lady's Slipper (*Cypripedium*), with a large pouch-like labellum, 2 fertile sta., a large staminode, and a three-lobed stigmatic surface.

FIG. 177.—Floral diagram of Orchidaceæ (Early Purple Orchis). The parts are shown in the positions which they occupy before twisting.

3. GRAMINEÆ

Annual or perennial herbs, with alt. distichous leaves having linear blades, long sheathing split bases, and ligules (p. 91 and Fig. 46 G); nodes swollen; stems hollow and jointed; intercalary growing points above nodes (p. 190). Branching takes place freely from nodes, resulting in some sp. in tufted growth. Unit of infl. a *spikelet* (Fig. 178 A and B), *i.e.* a small group of 1–5 sessile flrs. borne on a very short axis, with a pair of bracts (*glumes*, Fig. 178 *l.g.* and *u.g.*) at the base, which more or less enclose the flrs.; spikelets arranged in cpd. inflrs. which are either cpd. spikes (*e.g.* Wheat) or cpd. racemes (*e.g.* Oat). Individual flrs. arising in axils of bracts (termed *flowering glumes*, Fig. 178, *f.g.*), the tips of which often form long bristles or *awns* (Fig. 178, *a*); very low down on the peduncle each flr. bears a two-keeled bracteole (the *pale*, Fig. 178, *p*); the parts of the flr. till mature completely hidden between flowering

glume and pale. Flrs. reg., ☿, hypog., generally with A3 G(1) (see Fig. 178 C). Between the sta. and the flowering glume two small green fleshy outgrowths, the *lodicules* (Fig. 178, *ld.*), perhaps representing members of a reduced perianth. Sta. with long filaments and large, loosely hinged anthers (Fig. 178 A). Ov. sup., monocarp., with 1 ovule; stigma two-lobed and feathery (Fig. 178 A). Fruit an achene with pericarp and testa fused (pp. 36 and 279); seed alb., with embryo on one side (Fig. 18, I). Anem., mostly protog.

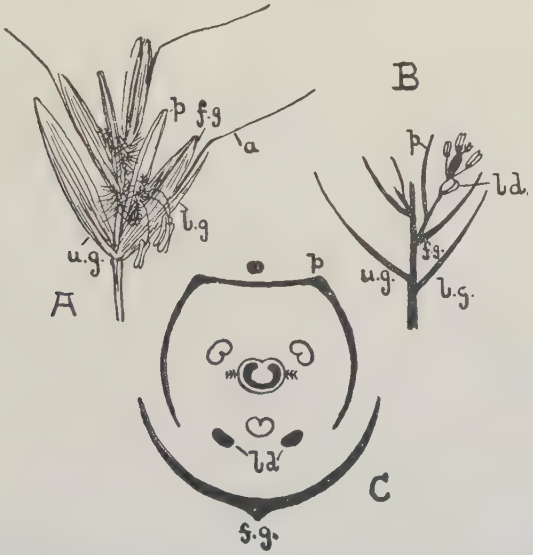


FIG. 178.—Structure of spikelets and flowers of Grass (Wild Oat). A, Complete spikelet with parts spread out. B, Diagram of a spikelet with all parts of axis elongated. C, Floral diagram. *a*, awn; *f.g.*, flowering glume; *ld.*, lodicules; *l.g.*, lower glume; *p*, pale; *u.g.*, upper glume.

The principal British genera are: Bent-grass (*Agrostis*), many sp. on heaths, with one-flowered spikelets; Foxtail-grass (*Alopecurus*), with a cylindrical compact infl.; Sweet Vernal-grass (*Anthoxanthum*), with unpleasing taste, flrs. appear very early and have only 2 sta., very typical of meadows; Oat (*Avena*), with long twisted awns, very susceptible to changes in the moisture of the air (p. 289); False Brome-grass (*Brachypodium*), in woods, flrs. with 2 or 3 sta.; Quaking-grass (*Briza*), on chalk-heaths, with ovate spikelets; Brome-grass (*Bromus*), with prominent awns; Dog's-

tail Grass (*Cynosurus*), on heaths, lower spikelets consisting only of glumes with a comb-like edge; Cock's-foot Grass (*Dactylis*), with all flrs. to one side, characteristic of meadows; Tussock-grass (*Aira*), on heaths, with two-flowered spikelets; Lyme-grass (*Elymus*), on sand-dunes, with a covering of wax on the leaves (p. 172); Fescue (*Festuca*), in meadows, with many-flowered spikelets; Manna-grass (*Glyceria*), with 2 aquatic sp.; Soft-grass (*Holcus*), one sp. in woods, the other on heaths, with hairy leaves; Barley (*Hordeum*), with very long rough awns; Rye-grass (*Lolium*), in meadows, infl. flat with spikelets in 2 rows; Melic-grass (*Melica*), in woods, with one- to two-flowered spikelets; Blue Moor-grass (*Molinia*), on moors and wet heaths, spikelets often purplish; Mat-grass (*Nardus*), on moors; Canary-grass (*Phalaris*), a common weed with egg-shaped infl.; Cat's-tail Grass, Timothy-Grass (*Phleum*), with toothed flowering glumes and cylindrical infl.; Reed (*Phragmites*), swamp-plant, sometimes 16 ft., lower flrs. in each spikelet ♂; Meadow-grass (*Poa*); Marram-grass (*Psamma*), on sand-dunes; Cord-grass (*Spartina*), on salt-marshes, with very large stigmas; Wheat- or Couch-grass (*Triticum*), with spikelets compressed at right angles to main axis.

The following genera are cultivated as cereals: Oats (*Avena*), Barley (*Hordeum*), Rice (*Oryza*), Rye (*Secale*), Millet (*Sorghum*), Wheat (*Triticum*), and Maize (*Zea*).

CHAPTER XXIV

Woodlands

We have so far considered plants separately, that is, as isolated units, but in nature they generally grow together in communities, the individual members of which not only mutually affect one another, but have to accommodate themselves to all the circumstances of their surroundings. These collectively, that is to say both the physical conditions (viz. those due to soil and climate) and those produced by other plants and animals, constitute what is termed the *environment* of the plant. We have already seen that there is a certain relation between the plant and its surroundings. Thus, plants growing in dry situations tend to reduce their transpiring surface (see Chapter XIII.), those growing in the shade place their leaves in the best position to receive light (pp. 83, 212), climbers depend upon the presence of a suitable support (p. 23), whilst animals are often necessary for pollination or seed-dispersal. The situation in which a plant grows, having regard to all the circumstances of its environment, is termed its *habitat*.

The different conditions afforded by the environment are spoken of as the *factors*, and these may be roughly classified into three groups: those due to the soil, those due to the climate, and those (biological factors) due to other plants and animals. Many of the soil-factors have already been considered (Chapter VI.),[1] among the most important being the texture, the amount of humus, the water-content, and the air-content, the last two depending more or less on the first two; to these we may add the chemical nature of the soil, in which respect the acid or alkaline character is probably most influential. Amongst the

[1] It will be advisable to read the chapter on the soil once again before proceeding with the subsequent matter.

climatic factors rainfall comes first, whilst, though the variation of temperature in different regions of the earth has a pronounced effect (cf. p. 198), it is relatively insignificant in small areas, except when we come to consider vegetation growing at different altitudes. The influence of light is very apparent where the growth is dense and one form overshadows another (see p. 197 and below). The degree of exposure to wind is another important climatic factor, specially marked on wind-swept coasts (Chapter XXVII.) and at high altitudes (see also p. 174).

Turning next to the biological factors, we need not at this point discuss the influence of plants upon one another, since that will be sufficiently apparent from the matter in this and the following chapters, but the relations between plants and animals deserve a little further attention. Apart from co-operation in pollination and seed-dispersal, the fact that plants afford a source of food to many animals may often greatly affect particular species. Thus, the ravages of Caterpillars may sometimes destroy a plant entirely in a small area (*e.g.* the Five-spot Burnet attacking Bird's-foot Trefoil), although such devastation by insects is much more extensive in warmer parts of the earth (*e.g.* by swarms of Locusts, or the Phylloxera-disease of the Vine). In correspondence with this, we have noticed that many plants possess means of defence, in the form of spines (p. 180), of distasteful substances (p. 137), of needle-like crysta s (p. 138), etc.; to these we may add the stinging hairs of the Stinging Nettle (Fig. 95 F) and the stiff, bristly or hooked hairs seen in many members of the Forget-me-not family (*e.g.* Comfrey, Fig. 95 E). Again, insects which produce galls (p. 202) sometimes bring about serious damage to crops (*e.g.* Turnip-fly). Other examples, in which the relation is reversed, are seen in the case of insectivorous plants (p. 149) and in the Salmon-disease.

The presence of characteristic plants in any particular situation is evidence of some benefit or benefits which they gain, either directly, through the nature of the soil or climate, or indirectly, through being removed from the sphere of competition with plants that, in other conditions, would prove more successful (cf. p. 315). But, whilst every habitat may be said to confer a benefit upon its legitimate inhabitants, it is equally true that adaptation to its special conditions is also involved, in particular

FIG. 179.—Interior of a Beech-wood, Pitstone Hill near Tring, Herts. Note the absence of undergrowth. [Photo. E. J. S.]

FIG. 180.—Ground-flora of a clearing in the Beech-wood shown above. The vegetation consists chiefly of Wood Sanicle, with Dog's Mercury in the foreground; on the right are two leaves of the Wood Burdock (*Arctium nemorosum*); just to the left of these is a plant of the White Helleborine, bearing three flowers. [Photo. E. J. S.]

[*To face p.* 310.

to those factors which are most pronounced. Thus, in any given locality that particular factor which is present in least amount, whether it be water, light, temperature, or the food-supply in the soil, will be the one that most profoundly affects its vegetation. For, if the other essential conditions are amply sufficient for most, if not all, of the species that normally inhabit the area concerned, the successful plants in the struggle for existence will be those best able to flourish with a small amount of the particular factor. Thus, the only forms that can live in a desert are extreme xerophytes that require little water, and further examples will be found in our subsequent consideration of woodlands (p. 312). It must be realised, however, that, although a certain plant may be eminently successful in conditions to which its structure is adapted, these very modifications may often render it unsuited to another environment (*e.g.* aquatics, succulents, cf. p. 181).

We shall begin our study of the social life of plants with a consideration of woodlands, because this type of vegetation has a designation which is at once used in popular parlance and further coincides with a botanical conception. No matter what woods we enter, all are characterised by trees as the most conspicuous feature of their vegetation. Beneath these, there are usually shrubs or smaller trees (Fig. 181), forming an *undergrowth* which is more or less dense according to the type of wood, and, on the ground, a carpet of herbaceous plants (the *ground-flora*, Figs. 180 and 182).

With differences in the type of predominating tree we get woodlands of various kinds which are usually associated with definite types of soil. Thus, on non-calcareous soils (cf. p. 64) one generally finds Oak- (*Quercus*) [1] or Birch- (*Betula*) woods, whilst calcareous soils frequently bear Beech- (*Fagus*) and Ash- (*Fraxinus*) woods. Where we have intermediate types of soils the woodlands may show a mixed character (*e.g.* the Oak-Ash-woods found commonly on marls). Hand in hand with such differences in the dominant (*i.e.* most important) tree, the kind as well as amount of undergrowth and ground-flora will be found

[1] In the case of plants not mentioned in Chapter XXIII., the generic name is given in brackets after the popular name. Where a plant is particularly characteristic, the specific name also is added.

to change. But whilst the component species may vary to such an extent that two woods have few forms of trees, shrubs, or herbs in common, yet those found in the one are replaced by similar types in the other, bearing the same relation to one another. Such a definite type of vegetation as woodland we can term a *formation* and the diverse kinds, such as Oak-woods, Ash-woods, etc., in which different species predominate, we shall speak of as *associations*. Later on we shall treat of other formations such as moorlands, sand-dunes, etc.

In utilising the woodland as an example of a plant-formation we have just seen that it is composed of three tiers, viz. the trees, the undergrowth, and the ground-flora. Amongst the conditions necessary for plant-life light has been shown to be a highly important one and, in the woodland, this is the factor which most markedly limits or restricts the kinds of plants that can occur in the undergrowth and ground-flora (cf. above). This is due to the production of a more or less dense canopy of foliage, either by the uppermost tier of trees or the second tier of shrubs, and as a consequence the character of the flora of a woodland depends largely on the amount of shade cast by the constituent members.

Of our woodland trees the Beech found on chalky soils in the south-east of England casts the deepest shade, owing to its extensive branching (p. 78) and perfect leaf-mosaic (p. 84). On entering such a wood we are struck by the paucity of vegetation upon the ground and the almost entire absence, except at the edge, of shrubby undergrowth (Fig. 179). The species, as well as the individuals, of the ground-flora are few, but, wherever there is a clearing (Fig. 180) or the trees are sparsely scattered, the sudden increase of vegetation shows at once that the soil is not at fault; owing to the slow rotting of the leaves, etc. of the Beech, there is, however, often not much available humus in such a wood. The commonest herb of the Beech-wood is the Dog's Mercury (*Mercurialis*, Fig. 180) and it is a significant fact that this is one of the earliest of our native plants to flower. Other frequent forms, mostly early-flowering and sometimes abundant in the better-lighted parts, are the Wood Sanicle (Fig. 180), the Dog and Hairy Violets (*Viola*), the Wild Strawberry, and the Enchanter's Nightshade (*Circæa*). A certain number of Orchids are usually found in Beech-woods,

FIG. 181.—Interior of an Ash-wood, Clifton woods, Bristol. The dense shrubby undergrowth is seen below, whilst in the fork of the tree in the foreground a plant of the Polypody is visible. [Photo. E. J. S.]

FIG. 182.—Ground-flora of a damp Oak-wood in early spring, Harpenden, Herts. The vegetation consists chiefly of Wild Hyacinth and Dog's Mercury. In the background are seen the stems of Hazel and Hornbeam forming the undergrowth. [Photo. E. J. S.]

[*To face p.* 312.

the most characteristic being the large White Helleborine (Fig. 180), whilst two saprophytes devoid of chlorophyll (viz. the Bird's-nest Orchid, Fig. 77, and the Bird's-nest) are often met with in the height of the summer, even in the densest parts of the wood, since these forms can flourish in deep shade. In the autumn their place is taken by numerous Fungi which grow in the humus formed by the fallen leaves. Where, as at the edge of the wood, we find a certain amount of shrubby undergrowth the most characteristic forms are the Hawthorn, the Wayfaring Tree (*Viburnum lantana*), the Dog-wood (*Cornus*), and the Old Man's Beard.

In marked contrast to the Beech-woods, but occurring on similar calcareous soils, particularly limestones, are those in which the Ash is dominant (Fig. 181). This tree casts very little shade and comes into leaf late in the season; in correspondence with these facts we usually find a varied and abundant undergrowth and ground-flora, though the extreme development of the shrub-layer may itself in some cases lead to the production of so dense a canopy as almost to prevent the growth of herbs beneath.

The amount of shade cast by the Oak is more or less intermediate between that cast by the Beech and Ash and, since Oak-woods are very common in many parts of England, they may be dealt with at some length. Two species of Oak are found in Britain, each of which forms woods on the appropriate type of soil. The most frequent kind, and that usually planted, is the Pedunculate Oak (*Quercus robur*) in which the leaves are glabrous on both surfaces and the lamina ends somewhat abruptly, at its point of insertion upon the petiole, in a pair of lobes with the margins slightly turned over (Fig. 183 A). The other species, the Sessile-fruited Oak (*Quercus sessiliflora*), bears star-shaped hairs on the under sides of its leaves and the blade tapers towards its insertion on the petiole (Fig. 183 B).

The Pedunculate Oak forms woods chiefly upon deep and heavy (p. 71) soils, such as clays and clayey loams, and the association to which it gives rise may be termed the *damp Oak-wood association* (Fig. 182). Other trees besides the Oak are frequently found and of these the commonest are usually the Wild Cherry, Birch, Maple (*Acer*), Ash, Holly (*Ilex*), and sometimes the Apple. In certain localities the Hornbeam (*Carpinus*)

is a prominent feature (*e.g.* in parts of Epping Forest), though frequently when it occurs it is coppiced (*i.e.* cut down periodically) and then forms the predominating feature of the undergrowth (*e.g.* on the stiff clays of North London). As a general rule, however, the shrub-layer consists mainly of Hazel (*Corylus*), amongst which commonly occur bushes of Hawthorn, Sloe, Dogwood, Willows, Roses, and Brambles, as well as the Honeysuckle (*Lonicera*).

The most frequent members of the ground-flora in such a wood, often forming large expanses (Figs. 182, 184), are the Wild Hyacinth (Fig. 184), Primrose, Lesser Celandine, Wood Anemone, Yellow Dead-nettle, Dog's Mercury (Fig. 184), and in less abundance the various kinds of Dog-violet. Of great

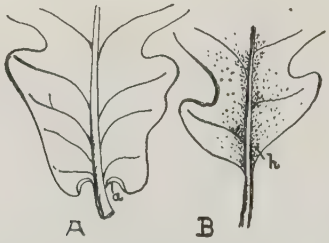


FIG. 183.—Portion of leaf of A, the Pedunculate Oak, and B, the Sessile-fruited Oak (about two-thirds natural size). *a*, basal lobe showing margin turned over. *h*, hairs.

frequency, but not forming such pronounced sheets, are a large number of species, the more familiar of which are the Bugle, Goldielocks (*Ranunculus auricomus*), Wood Sorrel (*Oxalis*), Barren Strawberry (*Potentilla fragariastrum*), Enchanter's Nightshade, Ground Ivy, Cuckoo-pint (*Arum*), and several Grasses (Melic, Vernal, False Brome Grass, etc.). In the Oak-woods of Kent the Milkmaid often covers large areas, whilst on the more loamy soils the Wood Sandwort, Woodruff (*Asperula*), Wood Sanicle, Wood Sage, Foxglove, and Bracken (*Pteris*) are conspicuous.

If we follow the story of the wood from the early days of spring to the fall of the year, we are at once confronted with the problem as to how the soil is able to accommodate and nourish so many individuals and such a constant succession of forms.

The solution is in part furnished by the subterranean architecture of the wood, for just as we find the aerial organs forming three definite tiers, each utilising the sunlight that has passed through the layer above, so too in the soil beneath we find a layering of the root-systems. Those of the trees and shrubs are naturally the deepest, whilst the shallow ones of Grasses and of some of the herbs are nearest the surface. The intervening layers are occupied by many roots, frequently belonging to plants with underground storage-organs, such as the Wild Hyacinth and Cuckoo-pint. In this way it is only the root-systems of plants situated in the same layer of soil that to any extent compete with one another, whilst owing to the successive development of the flora the overground shoots mainly compete with those produced at the same time.

Woodland plants probably receive a twofold benefit from their habitat, firstly in the form of shelter and secondly by the absence of sun-loving competitors (cf. p. 310). To any one who possesses a garden it is a familiar observation that the majority of plants in deep shade bloom either very sparsely or, more frequently, not at all (p. 197), and what is true of the garden-flowers is in general true also of the wild species. The early flowering of most woodland plants is to be related to the fact that at this time of the year the overhead canopy has not yet formed. Indeed all the commonest woodland plants, such as the Anemone, Dog's Mercury, Primrose, Wild Hyacinth, and Lesser Celandine, have finished blooming, and in many cases have formed their seeds, before the canopy is complete. Not only does the shade prevent the development of the flowers of most plants, but also, where these possess attractive mechanisms for insects, their conspicuousness would be to a great extent lost. It is probably in relation to this that many of the later-flowering woodland plants are highly scented, *e.g.* Woodruff, Honeysuckle, Butterfly Orchis, etc.

No less essential than the development of flowers, however, is the formation of food-material for growth and reproduction. It is therefore of supreme importance to the members of undergrowth and ground-flora that their leaves should be produced early, so that assimilation may proceed whilst light is plentiful. In many plants occupying other habitats the period of flowering and maximum growth does not take place till after

the first-formed leaves have provided the necessary material. But in a woodland the bulk of the growth and flowering is accomplished at the outset, and in relation to this we find that most members of the ground-flora are perennials possessed of some kind of storage-organ in which food-substances, elaborated during the previous season, are held in readiness to supply the material for growth and reproduction in the following spring. Examples are seen in the bulbs of the Wild Hyacinth, Daffodil

Fig. 184.—Ground-flora of a damp Oak-wood in early spring, Harpenden, Herts., showing Wild Hyacinths and Dog's Mercury. Locality same as in Fig. 182, but photograph on a larger scale.

(*Narcissus*), and Broad-leaved Garlic, the corms of the Cuckoo-pint and Winter Aconite, the tuberous roots of the Lesser Celandine, and the fleshy rhizomes of the Wood Anemone, Moschatel (*Adoxa*), and Enchanter's Nightshade.

After the flowering period is over and the interior of the wood has darkened, the leaves of most of its inhabitants, except such as the Moschatel and Lesser Celandine, persist, though the rate of photosynthesis is considerably reduced. The efficiency of the leaves in this respect is, however, to some extent compensated by further growth in area, so that a larger surface

is presented to the light (cf. also p. 197). The protection from wind and the heat of the sun afforded at this stage by the canopy above and the vegetation around, now probably makes this possible, since excessive transpiration is prevented. The

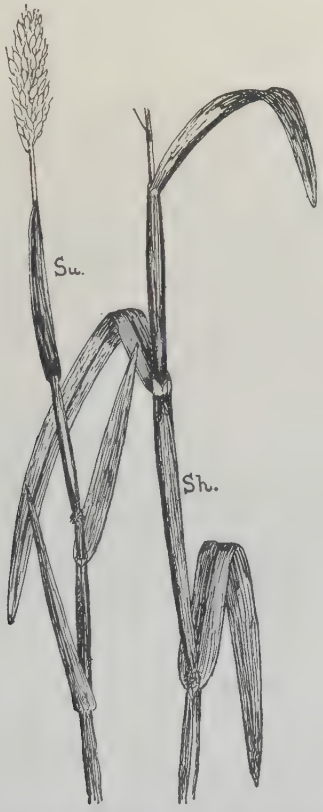


Fig. 185.—Sun- (*Su.*) and shade- (*Sh.*) forms of Wood Soft-grass (about two-thirds natural size).

long internodes of many woodland plants, to which we have already referred (p. 196), leads to a wide separation of the leaves and consequently little mutual overshadowing. Moreover, during development, the blades of such shade-plants take up the position best suited to receive the incident light (cf. p. 84),

excellent examples being afforded by the Bracken and Yorkshire Fog (Wood Soft-grass). Both these plants, when growing in bright sunlight, place their leaves at an acute angle with the direction of the sun's rays, thus minimising their effect (Fig. 185, *Su.*) ; in light of medium intensity, however, the blades of the Grass and the pinnæ of the Bracken are arranged so as to receive the light at right angles to the surface, whilst under the deep shade of trees the whole leaf bends over so as to absorb

FIG. 186.—Dry Oak-wood, lining the sides of a moorland valley in Yorkshire. On the left, in the foreground and elsewhere at the sides of the stream, are seen bushes of Alder. [Photo. E. J. S.]

the oblique rays that come in under the canopy of overhead foliage (Fig. 185, *Sh.*).

When the undergrowth of a wood has been coppiced, the increased access of light finds expression in the much greater vigour and larger amount of the ground-flora. The majority of Oak-Hazel woods are periodically coppiced at more or less regular intervals, so that the herbaceous vegetation waxes and wanes, being least when the undergrowth is thickest, and most abundant about the second or third year after coppicing. Sometimes, as has been mentioned, the Hazel is replaced by the Hornbeam as the chief constituent of the shrub-layer ; the

latter plant, which has a leaf-mosaic like that of the Beech (cf. Fig. 44), forms a much denser canopy and the result is a ground-flora poor in number of species and much resembling that of a Beech-wood.

Upon drier loams, sands, and shallow siliceous soils generally, the characteristic tree is the Sessile-fruited Oak, forming the *dry Oak-wood association*; the same tree also frequently gives rise to woods lining the sides of many of our rocky valleys (*e.g.* on the

FIG. 187.—Interior of a dry Oak-wood on slates, Wales, showing a ground-flora consisting almost entirely of Mosses. [Photo. E. J. S.]

slates of Wales and the sandstones of Yorkshire, Fig. 186). The characteristic species of the ground-flora in this association are the Bracken, Wood Soft-grass, Hair-grass, Wood Sage, Tormentil, Foxglove, Pretty St. John's Wort (*Hypericum pulchrum*), Great Woodrush (*Luzula*), Golden Rod, Hawkweeds, and Ferns. The shrubby layer shows few of the representatives found in the damp Oakwood, but Honeysuckle, Brambles, and Holly (*Ilex*) are often common. In the rocky districts above mentioned the ground-flora not infrequently consists almost exclusively of a carpet of Mosses composed of numerous species (Fig. 187).

On many of the heaths with light sandy soils (p. 71), Pine or Scotch Fir (*Pinus*) and Birch cover extensive areas, frequently occurring intermingled as colonisers in the heath-formation (cf. p. 323), every grade between woods and heath being found. Where the Pine-trees grow close together, they cast an extremely dense shade and the ground is usually devoid of vegetation, except for a number of Fungi in the latter part of the year and various Mosses, amongst which the grey tussocks of one known as *Leucobryum* are most conspicuous. When the Scotch Firs are less densely aggregated, a sparse vegetation appears which consists chiefly of Bracken, Whortleberry (*Vaccinium*), Heather (*Calluna*), Heaths (*Erica*), Tormentil, and occasional Grasses (particularly Tussock-grass), all in varying amounts. The greater the amount of light penetrating to the ground, the more numerous the heath-species that can survive. It may be added that typical Birch-woods are only found in the north of England and at high altitudes.

FIG. 189.—Heath, Hindhead Common, Surrey. A large proportion of the vegetation on the further slope consists of Ling; the plants on the horizon are Scotch Firs. [Photo. F. E. F.]

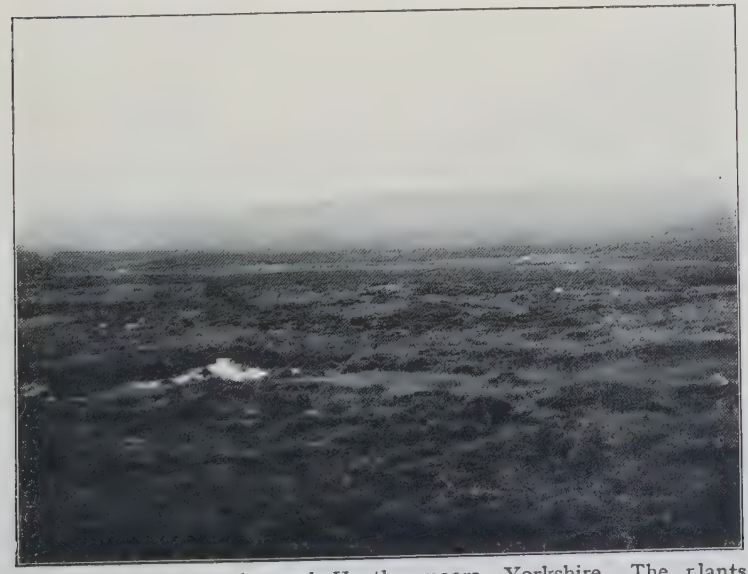


FIG. 190.—Distant view of Heather-moors, Yorkshire. The plants in the foreground are mainly Heather and Whortleberry, whilst the grassy patch consists chiefly of Cotton-grass and Rushes.
[Photo. E. J. S.]

[*To face p.* 320.

CHAPTER XXV

Heath and Moorland

Wherever woodlands have been cut down, in the drier parts of the country, their place is taken either by a scrub or a heath-association which differ in character according to the soil upon which they grow. Thus, on non-calcareous soils (p. 64) formerly occupied by Oak-wood, we often find a bushy *scrub* notable for the prickly nature of the component species and hence offering little inducement to browsing animals. Many of our so-called commons bear vegetation of this type, the Gorse being often one of the most conspicuous forms. Intermingled with it are numerous scattered bushes of Hawthorn and Blackthorn or Sloe, whilst the prickly scrambling stems of Wild Roses and Blackberries are everywhere frequent. Where the shrubby members are less abundant Grasses, such as the Rye-grass, Sweet Vernal-grass, Dog's-tail Grass, Bent, and Meadow Soft-grass are the dominant feature and form a kind of pasture. With these are associated a great number and variety of herbaceous perennials of which the most frequent are the Buttercups, Clovers, Plantains (*Plantago*), Sorrels, Cat's-ear, Bird's-foot Trefoil, etc.

On chalky soils the scrub (Fig. 188) consists also of Spindle-tree (*Euonymus*), Buckthorn (*Rhamnus catharticus*), White Beam (*Pyrus Aria*), Elder (*Sambucus*), Wayfaring Tree, Old Man's Beard, and Burnet Rose. The low-growing grass-land (*e.g.* of the chalk-downs) is usually dominated by Red Fescue, together with Quaking-grass, Giant Brome, etc., forming a close turf. One of the most striking features, however, of this type of pasture is the wealth of blossom in the early summer. The numerous chalk-loving plants which form these floral carpets include the Milkwort (*Polygala*), Purging Flax (*Linum*), Kidney-

vetch, Horseshoe-vetch, Salad Burnet, Wild Parsnip, Sheep's Scabious (*Scabiosa*), Dwarf Thistle, Clustered Bell-flower (*Campanula glomerata*), Squinancy-wort (*Asperula cynanchica*), Hardheads, and several Orchids; all of these are of low growth, except when flowering.

Much of the existing pasture would perhaps pass into scrub and eventually into woodland, but for the fact that its condition is artificially maintained by the constant browsing of wild or domesticated animals. The high winds in exposed situations

FIG. 188.—Chalk-scrub, Berkhamstead Common. The vegetation is mainly composed of Furze, Hawthorn (most of the large bushes in the background), and Blackthorn. In the foreground, on the right, is a mass of Old Man's Beard in fruit and, on the left, a bush of Buckthorn. [Photo. E. J. S.]

(*e.g.* mountain-tops, etc.) probably operate in a similar manner, so that there also we find grassland. Other causes contributing to the formation of pasture, both in these situations and elsewhere, are probably the small amount of humus, the alkaline character of the substratum, and the dry condition of the soil in summer.

Not infrequently, on comparatively dry soils such as sands and gravels, a *heath-association* (Fig. 189) develops, characterised by the presence of a usually shallow layer of relatively

dry peat (cf. p. 64) containing a considerable proportion of sand. The dominant plant is the Heather or Ling (*Calluna*), sometimes (especially on old heaths) almost pure, or accompanied by the Cross- and Fine-leaved Heaths (*Erica tetralix*, Fig. 191, and *E. cinerea*) and the Whortleberry or Bilberry (*Vaccinium*). Occasionally, as in parts of Bedfordshire and Surrey, such heaths become extensively colonised by the Scotch Fir (cf. p. 320) which may form a dense growth tending to kill off the heath-flora.

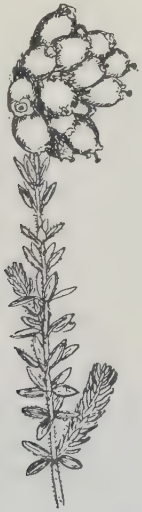


Fig. 191.—Portion of a plant of the Cross-leaved Heath *Erica (tetralix)* (natural size).

The typical heath, owing to the deep shade cast by the richly branched Ling, has a relatively scanty flora, sometimes consisting apart from the dominant plant almost entirely of Mosses and Lichens. Where the heath is not so pure the commonest associates of the Heather, in addition to Heaths and Bilberry, are the Dwarf Furze (*Ulex nanus*), Broom, Tormentil, Heath Bedstraw (*Galium saxatile*), Heath Speedwell (*Veronica officinalis*), Woodsage, Juniper (*Juniperus*), and Bracken, as well as various Grasses of which the Hair-grass (*Aira flexuosa*) is the most characteristic. The parasitic Dodder (*Cuscuta*, p. 141 and Frontispiece)

is also not uncommonly found attacking numerous members of the heath-association.

In the wetter parts of the heath a slightly thicker layer of peat is met with, bearing particularly the Whortleberry and sometimes the Bog-moss (*Sphagnum*). The vegetation in such habitats is transitional to that of typical moorland (cf. below).

The soil of a heath is very shallow and generally sandy; moreover, the surface-layer of peat, owing to the large quantity of moisture which it absorbs, largely prevents the access of rain-water to lower levels, so that most of it evaporates again in subsequent warm weather. The peat further absorbs the heat-rays of the sun, so that the surface becomes very warm on a sunny day, a fact which is familiar from the quivering of the air just above the ground at such times. Most heaths finally are exposed and wind-swept. As a result of all these factors the different members of the heath-flora are all xerophytes, many of them forming rolled leaves (*e.g.* the Heather and Heath, cf. p. 176 and Fig. 96 C and D) or exhibiting other means of transpiration-reduction (spines in the Furze, leathery leaves in the Whortleberry, cf. p. 172, reduction of leaves in the Broom, etc.). Moreover, a considerable number of the typical heath-plants are evergreens, since conditions are scarcely more unfavourable in winter than in summer.

The upland *moors* (*e.g.* those of Yorkshire, Fig. 190) are probably to be regarded, like the majority of heaths, mainly as products of soil formerly occupied by woodland which has been destroyed, either by man or natural agencies. For, just as heath replaces woodland in the drier districts, so is moorland found on the site of former forest in those parts where a moderately high rainfall usually obtains. That many of our moors have thus taken the place of woodland can often be seen from the presence of tree-trunks, mostly of Birch, embedded in the peat (Fig. 192). Lowland moors, such as those of the New Forest, on the other hand, appear to have developed from fens (cf. p. 340).

Moors are usually characterised by a soil having a greater depth of peat than heaths and a smaller percentage of intermingled sand, so that the soil has an increased water-retaining capacity. In the wetter parts the peat may attain to consider-

FIG. 192.—Section of peat on a Yorkshire moorland, showing embedded trunks of the Birch. The vegetation on the slope above consists of Ling and Bracken. [Photo. E. J. S.]

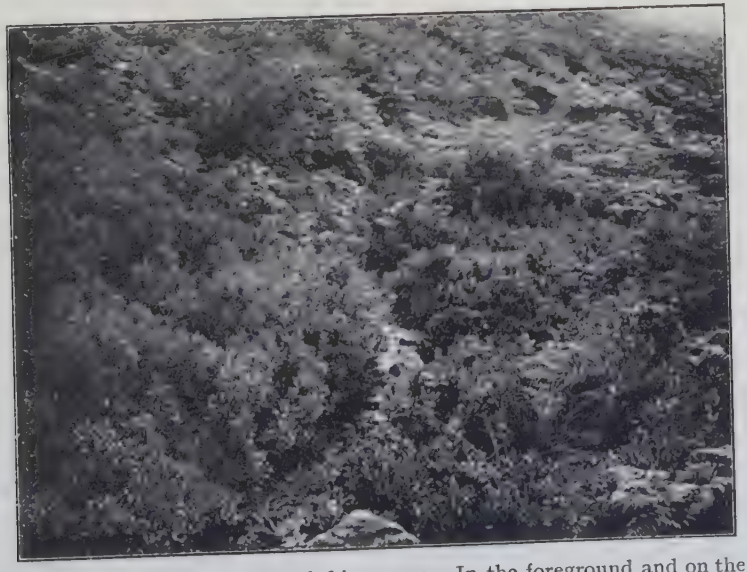


FIG. 193.—Wet part of a Yorkshire moor. In the foreground and on the left is a dense growth of Bog-myrtle, whilst in the background a considerable quantity of Bracken is seen. [Photo. E. J. S.]

[*To face p.* 324.

able thickness, as a result of the presence of the Bog-moss by which it is very rapidly formed. Owing to the large amount of acid humus present, the soil-water of the moor is acid in its reaction and thus contrasts very markedly with the alkaline character of fen-water (cf. p. 346).

In the commonest type of moorland, namely the *heather-moor* (Fig. 190), the dominant plants, amongst which Heather, Heath, and Whortleberry (all members of the Heather-family or Ericaceæ) are most prominent, all possess xerophytic foliage, whilst most are devoid of root-hairs, the function of which is taken over by fungal threads (cf. p. 146). In view of the soil being relatively wet, the xerophytic character is somewhat surprising, but probably the acidity of the soil-water, the poor aeration owing to its water-logged character, and the low temperature of the substratum, all tend to lower the rate of absorption by the roots. Moreover, moorlands are usually to be found in more or less exposed wind-swept situations. The retentive capacity of the peat for water may also play a part, but this is to a large extent compensated by the heavy rains and mists in the districts where moors occur.

The commonest of the shrubby associates of the Heather on such a moor are the Fine-leaved and Cross-leaved Heaths (Fig. 191), the Crowberry (*Empetrum*), and the Whortleberry. These together form a vegetation with somewhat low growth and of a more or less even level, so that the plants afford one another mutual protection. The last-named of these shrubby forms has deciduous leaves with a thick cuticle and becomes a switch-plant in winter (cf. p. 176), whilst the remaining plants have rolled leaves. Other frequent constituents are the Blue Moor-grass, the Mat-grass, the Bog-rush (*Juncus squarrosus*), the Heath Bedstraw, the Bracken, and the Hard-fern (*Blechnum*), besides numerous Mosses of which the Hair-moss (*Polytrichum*) is the chief. In the damper parts (Fig. 193) the insectivorous Sundew and Butterwort (Fig. 82) flourish, together with Sweet-gale or Bog-myrtle (*Myrica*), Cranberry (*Vaccinium oxycoccus*), Bog Asphodel, Marsh Violet, Lesser Spearwort (*Ranunculus flammula*), Cotton-grass (*Eriophorum*), various Rushes, Sedges (*Carex*), and the Bog-moss.

It is more particularly in the wetter situations that the Whortleberry finds its chief home, here frequently becoming

the dominant plant. In some areas, where the peat is still deeper and contains a much smaller quantity of sand than in the heather-moor, an extremely wet soil results bearing an association dominated by the Cotton-grass (*Cotton-grass moor*). This plant, which forms peat with very great rapidity, has narrow leaves with a very thick cuticle and is thus suited to exposed situations, whilst its rhizomes traversed by numerous air-canals enable it to grow in a soil that is completely water-logged.

The different types of moorland-associations appear to be determined mainly by the water-content of the soil, and this is dependent on the depth of the peat and the amount of intermingled sand, the latter being usually least when the former is greatest. Thus, the relatively dry heather-moor is formed on peat containing a considerable quantity of mineral substance and with a depth ranging from about 1 to 4 feet. The very wet Cotton-grass moor, on the other hand, is associated with peat having a very small mineral content and attaining a depth of from 5 to as much as 30 feet.

Whilst the influence of man is no doubt largely responsible for many of our heaths and moors, it is mainly in the meadow and arable land floras that the artificial factor is most marked. The vegetation of *meadow-land* is more or less dependent upon the character of the natural Grass-association on the soil where it occurs, including in chalky districts a number of chalk-loving plants (cf. p. 321) which are mostly absent in meadow-land on non-calcareous soils. The plants of the meadow are, however, profoundly affected by mowing, the grazing of animals, and the type of manuring employed. The meadow differs from upland pasture chiefly in the damper type of soil which, moreover, is often alluvial in character and periodically flooded.

The members of the meadow-flora are nearly all perennial herbs exhibiting relatively low growth and including a preponderance of Grasses (*e.g.* Cock's-foot, Timothy, and Foxtail), with which, however, a great variety of other plants are associated. Thus, the meadow (Fig. 194) is the characteristic home of the Buttercups and Clovers, and of such forms as the Milfoil (Yarrow), Daisy, Dandelion, Sorrel, etc. and, on poorer soils, the semi-parasites (p. 139). In the meadow the underground water-table is never far from the surface and, as it comes to lie

higher and higher, we get more and more of an approximation to a marsh (see next chapter).

Associated with the relatively bare and broken surface of *arable land* are a number of plants that can be classed together as weeds and which here find their chief home. Nearly all are annuals of quick growth and readily reproducing by seed for

Fig. 194.—Vegetation of a meadow. The chief plants seen are Dutch Clover, Buttercups, Daisies, Yellow Rattle, and numerous Grasses. [Photo. E. J. S.]

which they possess an efficient means of dispersal. Such are the Shepherd's-purse (Fig. 1), Shepherd's-needle, Field Buttercup, Knot-grasses (*Polygonum*), Poppy (*Papaver*), Fumitory (*Fumaria*), Charlock, Field Spurrey, Medick, Field Lady's-mantle, Field Madder (*Sherardia arvensis*), Groundsel, Thistles, Sow-Thistle, Corn Marigold (*Chrysanthemum segetum*), Hemp-nettle, Goose-foot (*Chenopodium*), Scarlet Pimpernel, etc.

CHAPTER XXVI

Marsh- and Water-Floras

In low-lying meadows we find considerable variation in the depth at which the underground water-table is situated (cf. p. 326) and, where the latter approaches near to the surface, any depression may furnish a *marsh-flora*, such as is found more particularly round the edges of lakes and ponds and by the sides of sluggish streams. In a marsh of this character the ground is almost completely permeated by water, so that the underground organs of the plants inhabiting it may be said to be nearly submerged, but there is, for the greater part of the year, no free water apparent above the soil. In such situations (Fig. 195) we find typical marsh-plants, the more characteristic being the Marsh Marigold, Water-mint, Ragged Robin (*Lychnis flos-cuculi*), Water Forget-me-not (*Myosotis palustris*), Milkmaid, Marsh Thistle (*Cnicus palustris*), Marsh Ragwort, Meadow-sweet, Marsh Horsetail (*Equisetum palustre*), Rushes (*Juncus*), Sedges (*Carex*), and Small Valerian (*Valeriana dioica*); if the soil is somewhat peaty, one meets with additional forms, such as Lesser Spearwort (*Ranunculus flammula*), Pennywort (*Hydrocotyle*), Lousewort, Water Blinks (*Montia*), Marsh Violet (*Viola palustris*), Devil's-bit Scabious (*Scabiosa succisa*), and Sneezewort (*Achillea ptarmica*).

Further towards the open water we come to a *swamp-flora* (Fig. 196) in which a certain amount of standing water is usually present above the soil-level, the vegetation often showing a more or less marked zonation corresponding to the depth to which the soil is submerged. In typical cases three such zones are distinguishable. Beginning with the Sedge-zone on the landward side, there follows a belt of Reeds, which is again succeeded by a zone of Bulrushes next the open water. Among the more

characteristic forms of the Sedge- and Reed-zones are the Iris, Flowering Rush (*Butomus*), Bur-reed (*Sparganium*), Water Plantain (*Alisma plantago*), Reed-mace (*Typha*), Spike-rush (*Heleocharis*), Reed Canary-grass (*Phalaris arundinacea*), Manna Grass, Great Water Dock (*Rumex hydrolapathum*), Water Dropwort, Purple Loosestrife, Hemp Agrimony, Gipsywort, Brooklime (*Veronica beccabunga*), Bog-bean (*Menyanthes*), and Smooth Naked Horsetail (*Equisetum limosum*). In the third zone the

FIG. 195.—Marsh-flora, Harpenden, Herts. In the foreground are seen various Sedges with Marsh Marigolds and, more particularly in the background, the leaves of the Meadow-sweet. [Photo. E. J. S.]

only common associate of the Bulrush is the Mare's-tail (*Hippuris*, Fig. 197).

Although the preceding lists roughly indicate the zonation, the individual plants locally show considerable differences in distribution, so that they are not always necessarily found in the belt mentioned; thus, some of the marsh-plants are commonly met with in the swamp-flora and *vice versa*. Moreover, in many cases only one or other of the zones is apparent, their occurrence depending largely on the rapidity with which the floor slopes.

A striking feature of the swamp-flora is the prevalent upright habit and the vertical position of the leaves of the constituent plants (Fig. 196); this probably makes it easier for the dense vegetation to bend readily under sudden gusts of wind without one plant injuring another.

As soon as we enter the region with free-standing water *aquatics* begin to appear, so that many of them are found among the members of the swamp-flora (cf. Fig. 196,

Fig. 198.—White Water Lily growing amongst Reeds (*Phragmites*), Wicken Fen, Cambridge. The floating leaves and flowers of the former are seen. [Photo. E. J. S.]

Fig. 198). Moreover, these aquatics themselves exhibit a zonation, again depending on the depth of the water. Near the shore we find forms rooted to the bottom and developing floating leaves, but, as the water deepens, we gradually reach the limit of depth from which they can bring these leaves to the surface and beyond this point they are absent. Examples are furnished by the White (*Nymphæa*, Fig. 198) and Yellow Water Lily (*Nuphar*), Water Starworts (*Callitriche*), Water Crowfoot (*Ranunculus aquatilis*), Floating Pondweed (*Potamogeton natans*).

and the Amphibious Bistort (*Polygonum amphibium*). In this same zone we get other rooted plants, such as the Arrowhead (*Sagittaria*) and the Water St. John's Wort (Fig. 196), which raise some of their leaves into the air, and still others, in which only the flowers appear above the water-level, *e.g.* Floating Bur-reed (*Sparganium natans*), Water Violet, and Water Milfoil (*Myriophyllum*, Fig. 201), the first two occurring in relatively shallow water. Amongst all these forms are found a number of free-floating (*i.e.* not fixed) aquatics, such as the Duckweed (*Lemna*), Frog-bit (*Hydrocharis*), Water Soldier (*Stratiotes*), and Bladderwort (*Utricularia*), the Water Soldier, however, being rooted to the bottom at certain times of the year.

Beyond the belt of floating aquatics which, starting from the shore, extends into considerably deeper water than the Bul-rush-zone of the swamp-flora, we get a number of typical sub-merged forms which can exist at a still greater depth. Such are many Pondweeds (*Potamogeton*), the rootless Hornwort (*Cerato-phyllum*, cf. Fig. 197), and the Canadian Pondweed (*Elodea*). At a still greater depth all aquatic flowering plants disappear and we only find Stoneworts (*Chara*) and subsequently nothing but thread-like pond-scums (Algæ) ; the latter occur in varying quantity in all parts of the water at certain times of the year.

In the case of streams the rate of flow greatly affects the character of the aquatic flora. Thus, where the current is rapid, there is an entire absence of free-floating forms, whilst many species that in quiet water grow above the water-level are completely submerged (*e.g.* the Arrowhead, Water Parsnip). Floating leaves are not developed in such a habitat, except near the edges where the flow is less rapid. The flora of a stream appears also to be markedly affected by the kind of rocks through which it flows.

The submerged parts of all water-plants are surrounded by a medium which is very different from that enveloping the over-ground organs of the ordinary land-plant. In the first place, it is far denser than air and consequently lends considerable support to the plants inhabiting it. Aquatics therefore lack an extensive supporting skeleton, such as that found in the land-plant (cf. p. 99 et seq.). In fact the principal strain to which the former are subjected is, as in the roots of terrestrial plants (cf. p. 8), a longitudinal pull due to currents in the water.

Hence we find that such mechanical tissue as the aquatic possesses is arranged in the same way as in a root, viz. as a central core (cf. Fig. 103).

In the second place, the surrounding water contains a far smaller supply of the Oxygen necessary for respiration (cf. p. 183) than an equivalent volume of air, so that breathing is attended with considerable difficulty in aquatics; carbon dioxide, on the other hand, is more readily dissolved by water and the aquatic consequently has a larger amount at its disposal, bulk for bulk, than a land-plant. Since, however, there are no pores on the submerged parts, both Oxygen and carbon dioxide have to enter by diffusion through the very thin cuticle, in itself a slow process.

The difficulty in breathing is compensated by very thin foliage or extreme division of the leaves (Figs. 199, 201), *i.e.* the creation of a large absorptive surface. Further, an atmosphere consisting largely of Oxygen is produced within the plant during photosynthesis which, owing to the relatively large amount of carbon dioxide, goes on readily; the Oxygen formed does not escape into the water, but passes into the numerous large canal-like air-spaces which traverse all parts of the aquatic (Fig. 103). When we demonstrated that an assimilating water-plant gives off Oxygen (cf. p. 133 and Fig. 70), we really collected some of this gas escaping from its *internal atmosphere*. The presence of these air-chambers furthermore gives the aquatic considerable buoyancy and thus helps to maintain it in an erect position in the water.

The underground organs of marsh- and swamp-plants suffer from the same difficulty in obtaining Oxygen and consequently possess a similar extensive system of air-canals which are continued also into the aerial parts. A few members of the swamp-flora (*e.g.* Gipsy-wort, Purple Loosestrife) sometimes develop a special aerating tissue on their submerged stems and roots, this appearing as a white spongy swelling on the parts concerned.

A third condition, which life in water involves, is the reduced illumination to which submerged aquatics are exposed, due to much of the light being reflected from the surface, whilst the remainder gets rapidly absorbed as it penetrates to deeper and deeper levels. For this reason, it is imperative for most water-plants to bring their assimilatory organs relatively near to the

FIG. 196.—Swamp-flora, Wisley. The vegetation consists of a thick growth of Water St. John's Wort (*Hypericum elodes*), amongst which is seen the Spike-rush on the right and the Pendulous Sedge on the left. [Photo. E. J. S.]

FIG. 197.—Aquatic flora, Water-end, Herts. Numerous upright shoots of the Mare's-tail are seen projecting from the water, in which the patches indicate the position of submerged plants of the Hornwort. In the middle the floating rosettes of the Water Starwort.
[Photo. E. J. S.]

[*To face p.* 332.

surface, and it is this which determines the depth at which submerged aquatics can grow. Naturally this depends to some extent on whether the water is clear or muddy.

A last feature of aquatic life is the abundant supply of water and often of mineral salts as well. This enables exceedingly rapid and prolific growth to take place, a fact which is strikingly illustrated by the Canadian Pondweed. This plant was introduced into this country in 1841 and spread with such rapidity that at one time it constituted a serious pest by choking up canals and other water-ways. In the aquatic, absorption of moisture is carried on over the whole surface and, as a result, the roots serve almost only for attachment and are little branched, whilst the water-conducting system (the wood) is poorly developed, few if any vessels being present.

The *submerged foliage* of water-plants consists, as already mentioned, either of very thin or of deeply divided leaves, the latter type being well seen in the Water Milfoil (Fig. 201), the Hornwort, and the Water Crowfoot (Fig. 199). Such deep division is not only of advantage in affording a larger surface for the absorption of carbon dioxide, but is also mechanically sound, since currents flow readily between the segments of the leaves without doing them harm. The long linear undivided leaves of the Fennel-leaved Pondweed (*Potamogeton pectinatus*), which readily trail out with the current, are equally well adapted to these ends. Occasionally submerged leaves have a broader surface, as in the Transparent Pondweed (*Potamogeton lucens*) where, however, the leaves are very thin and flexible.

Aquatics which produce floating leaves, as a rule also have a varying number of submerged ones; the latter are of one of the types just mentioned and generally quite different from the floating leaves, the most notable exception being the Yellow Water Lily, where they are similar in form but very much thinner. The difference between submerged and floating leaves is well illustrated by the Water Crowfoot (Fig. 199) in which the submerged ones are much divided and feathery, whilst those floating at the surface are reniform. In the White Water Lily the few submerged leaves are generally ribbon-shaped, whilst the floating ones are deeply cordate with a roughly oval lamina (Fig. 198). A particularly interesting example is afforded by the Arrowhead (Fig. 200) in which, in still

water, three kinds of leaves are produced: firstly, ribbon-shaped submerged ones (Fig. 200 A); secondly, lanceolate or cordate floating ones, often with a deeply notched base (Fig. 200 B); and thirdly, sagittate aerial leaves (Fig. 200 C) standing out of the water; in running (cf. p. 331) or very deep water, however, only the submerged type of leaf is produced. In the Mare's-tail the aerial and submerged leaves are similar in form,

Fig. 199.—Portion of a plant of the Water Crowfoot (about two-thirds natural size), showing floating and submerged leaves.

but the latter are much longer, thinner, and more flexible than the former.

Floating leaves (Figs. 198, 199, 200 B) agree in mostly having an entire edge and in the fact that the petiole is attached more or less near the centre of the glabrous blade (cf. especially Fig. 198), so that the pull of the leaf-stalk acts centrally and the lamina is kept flat on the surface of the water. The floating leaves of the Water Lilies, moreover, have very long petioles, whereby the blade is brought to the surface, even in relatively

deep water, and enough play is allowed for currents to carry it to and fro without submerging it.

In the Floating Pondweed and the Amphibious Bistort, on the other hand, the petioles are short, the blades in this case being brought to the surface by the elongation of the stem. In

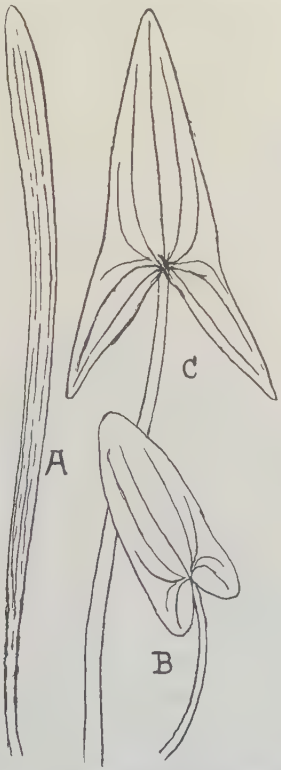


FIG. 200.—Different types of leaves of the Arrowhead (considerably reduced). A, submerged. B, floating. C, aerial.

these two plants the floating leaves are seen to be separated by much shorter internodes than the submerged leaves, a fact which is also apparent in the Water Crowfoot and more particularly in the Water Starwort. In the latter the opposite leaves on the submerged part of the stem are borne at widely separated nodes, but at the water-surface the internodes are scarcely developed.

the leaves being crowded together to form the familiar floating rosettes (Fig. 202, *W*). The longer internodes of the more deeply submerged portions of the stem in these plants are probably to be related to the reduced light-intensity, a feature which may also be responsible for the thin texture of the submerged foliage in many aquatics.

Floating leaves, unlike the submerged ones, bear stomates

FIG. 201.—Portion of a plant of the Water Milfoil, showing the inflorescence (consisting of four female flowers at the base and male flowers above) supported by the parachute-like arrangement of the whorled leaves (about natural size).

(p. 116) which are, however, restricted to the upper surface, the latter usually having a covering of wax (not developed over the pores) which prevents wetting and consequent blocking of the pores. By means of the latter the floating leaf maintains a connection between the air-spaces of the submerged portions of the plant and the outside atmosphere. The most important function of floating leaves, however, appears to be that of forming

a supporting platform around the base of the aerial inflorescence (cf. Fig. 199). The same purpose is fulfilled in some forms having only submerged foliage (*e.g.* Water Violet, Water Milfoil) by a parachute-like arrangement of the whorled leaves (Fig. 201) just beneath the water-level.

The roots of water-plants are generally all adventitious, forming white slender little-branched structures functioning mainly as organs of attachment (p. 333). Some aquatics even have no roots at all (*e.g.* Hornwort and Bladderwort). In free-floating forms, such as the Duckweed and Frog-bit, the roots dangle down into the water and in these cases not only absorb, but also serve like a weighted keel to keep the plant properly balanced in the vertical position.

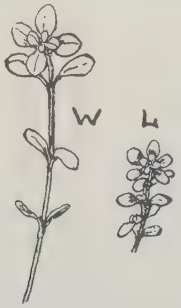


FIG. 202.—Land-form (*L*) and Water-form (*W*) of the Water Starwort (natural size).

A certain number of aquatics (*e.g.* Water Starwort, Water Crowfoot, Water Milfoil) are able to grow on damp mud, but such *land-forms* differ appreciably from the water-forms. In the first place, the internodes become extremely short, so that the whole plant is very stunted (cf. Fig. 202, *L*); further, the leaves are much thicker and smaller (Fig. 202, *L*) and, when divided, show broader and fewer segments, whilst the roots are more strongly developed. As regards the internal structure, such a land-form shows far smaller air-spaces, an increase of water-conducting tissue, and a thicker cuticle, whilst stomates are present in the leaves. The Amphibious Bistort is peculiar in being able to grow equally well on dry land and as a floating aquatic, the land- differing from the water-form in having sessile hairy leaves and an upright self-supporting stem.

In view of their prolific growth vegetative reproduction is generally a great feature in aquatics. The simplest method is a mere detachment of branches which grow into new plants. This is very common in the Canadian Pondweed and the Hornwort; the latter owing to its brittle character readily breaks up and only rarely reproduces by seeds. With the approach of winter many forms produce so-called *winter-buds* (Fig. 203), *i.e.* ends of shoots in which the leaves are very closely crowded together and filled with starch (*e.g.* Hornwort, Canadian Pondweed, Fig. 203 A, Water Milfoil, Fig. 203 B); a considerable number of these are formed by each plant and, when the parent dies away, they sink to the bottom and, in the following spring, give rise to new individuals. These winter-

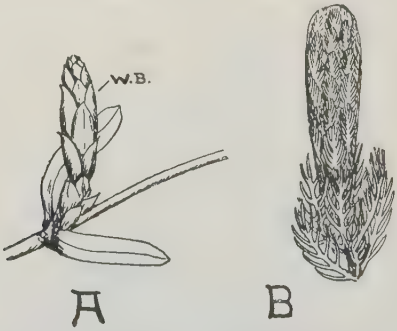


FIG. 203.—Winter-buds of A, the Canadian Pondweed, and B, the Water Milfoil (slightly enlarged). *w.b.*, winter-bud.

buds resemble the summer-buds (cf. p. 95) of land-plants in having no bud-scales which are unnecessary as there is no risk of drying up; on the other hand, they are often copiously covered with slime or mucilage.

The buds of the Frog-bit and the Water Soldier are formed at the ends of long more or less horizontal runners and are produced, not only in the autumn, but also during the summer, when they serve merely for vegetative propagation. Other methods of persistence during the winter are seen in the Duckweed, in which the plants often become full of starch in the autumn and sink to the bottom, and in the Arrowhead, in which small tubers are carried out on branches of the rhizome and are thus buried in the mud. In a mild winter, moreover, many

water-plants (Canadian Pondweed, Duckweed, Water Starwort) remain almost unaltered.

The bulk of aquatics raise their flowers above the water-level and thus betray their derivation from terrestrial plants. Some of them are entomophilous (*e.g.* Yellow Water Lily or Brandy Bottle, Water Crowfoot, Fig. 199, Water Violet, Arrowhead), whilst others are anemophilous (*e.g.* Water Milfoil, Fig. 201, Pondweeds, Fig. 139*) or perhaps occasionally pollinated by insects (*e.g.* Water-gnats) frequenting the surface of the water. In a large number of cases the peduncles bend after flowering is over and carry the developing fruits under water, so that they are well protected.

A few aquatics have become so highly adapted to life in water that they even produce submerged flowers (*e.g.* Hornwort, some Water Starworts). In the Hornwort these flowers are developed in the axils of the leaves and have but a small perianth, so that they are very inconspicuous. They are unisexual with both sexes on the same plant; the male flower has from twelve to sixteen stamens, while the female has a superior ovary composed of one carpel with a single ovule. In all such water-pollinated forms the pollen grains are smooth and float readily in the water, currents carrying them to the stigmas; pollination is therefore as uncertain as in anemophilous plants and, in correspondence with this, a considerable amount of pollen is formed. It may be added that many aquatics, which ordinarily raise their flowers above the water, fail to do so if, just before the time of flowering, rain is plentiful, so that the water-level rises rapidly; under these circumstances the flower-buds do not open and are cleistogamic (p. 277).

Many of the plants growing by the water-side have fruits which float readily and are not damaged by prolonged submergence. In this way they become distributed by water-currents.

The swamp-flora is always encroaching upon the aquatic vegetation and in a similar way the reed-swamp, as it becomes more and more dense and the level of the floor rises, is invaded by the marsh-flora. In East Anglia large areas are covered by such dense reed-swamps in which the predominating plants are Sedges and Grasses, *e.g.* Bog-rush (*Schoenus*), Twig-rush

(*Cladium*), Reed, Blue Moorgrass, Reed Canary-grass, etc. A certain amount of peat is formed in such situations, but this contains a large proportion of mineral substance and the soil-water, unlike that of the moorland (cf. p. 325), is alkaline. This type of association is known as a *fen*, other characteristic plants being the Meadow-sweet, Ragged Robin, and Valerian.

Eventually the soil built up in this way, by the accumulation of organic material, may become colonised by trees, such as Buckthorn, Alder (*Alnus*), Willow, etc., and a fen-wood or *carr* is produced. In a similar manner the ordinary marsh-plants may serve as the ground-flora of a woodland in which Alder and Willow predominate.

CHAPTER XXVII

The Sea-shore

The flora of the coast affords types of vegetation quite distinct from those we have hitherto considered, for, whether judged by the plants themselves or the situations in which they live, the beach, the sand-dune, and the salt-marsh represent plant-formations which have little in common with those occurring inland. If we walk along the shore of a rocky coast we are at once impressed by the wealth of *Seaweeds* which flourish in the region between tidal limits. Below the level of the lowest tides there is abundant plant-life consisting chiefly of Brown or Red Seaweeds, the latter being in the majority ; above low-tide level we find a rich vegetation of Green forms with considerable numbers of Brown ones (often the Bladder-wrack), these latter becoming more and more abundant as we approach the high tide limit. The slippery character of many of the Seaweeds is due to the presence of abundant slime or mucilage, which helps to retain moisture and so minimises the effect of alternate submergence and drying up to which all forms living between tide-limits are exposed.

The *Beach* itself, above high-tide level, is not infrequently composed of more or less water-worn fragments or pebbles forming a fringe of shingle to the shore (*e.g.* at Pevensey, Hove, and Llandudno) or constituting a bar or spit (*e.g.* the Chesil Bank and Hurst Castle Bank). Inhospitable as these situations seem, exposed as they are to the full force of the wind, and with a barren soil composed of shingle, sand, and a small amount of drift (*i.e.* plant-remains cast up by the sea or from the salt-marshes behind), yet such habitats afford the chief home of many plants that are almost or entirely confined to such localities. Amongst the commonest may be mentioned the Yellow Horned

Poppy (*Glaucium*), Wild Beetroot (*Beta*), Sea Campion (*Silene maritima*), Sea Purslane (*Arenaria peploides*), and Crisped Dock (*Rumex trigranulatus*); more locally the Shrubby Sea Blite (*Sucæda fruticosa*), Sea-kale, and the Maritime Pea (*Lathyrus maritimus*) are conspicuous features. Most of these plants have deep roots and fleshy leaves.

The controlling conditions upon the pebbly shore or shingle bank are primarily those of the soil with its extreme mobility,[1] small amount of humus, and lack of capacity for water-retention. The vegetation appears to depend for its existence largely upon a regular supply of humus to the shingle and, as a consequence, fringing banks which only receive a small amount of drift from the sea are often very bare, whilst those forming a bar or spit exhibit more extensive vegetation, as a result of the more abundant humus derived mainly from the marshes behind. Moreover, the plants inhabiting a pebble-beach are at times partially buried under the shingle carried up during storms, and their presence in such habitats is only possible owing to their capacity for growing through to the new surface. The vegetation is in great part perennial and of low growth, only developing a tall erect stem, if at all, at the time of flowering. After the seeds are shed the upper parts die away, so that during the stress of winter and the winds of early spring the foliage appears either as a rosette closely pressed against the ground (*e.g.* Horned Poppy), or takes the form of winter-buds situated upon the subterranean portion of the stem (as in the Sea Purslane).

Exposure to wind is a general feature of coastal situations and is shared equally by the beach, sand-dune, and salt-marsh. The *sand-dune* (cf. Plate VII.) has much in common with the shingle bank, but the smaller size of the particles, whilst rendering the soil more retentive of water, vastly increases its mobility. This shifting character is indeed the dominant factor determining the vegetation of the dune as a whole.

In any locality where sand-hills abound (*e.g.* Southport, Winterton) it will be noticed that those nearest the sea are small and bear very little vegetation (Fig. 204); as we pass landwards, however, the dunes become larger and merge one into another, whilst the clothing of vegetation becomes more

[1] Where the shingle is relatively stable, small Lichens of a black or grey colour often cover the surface of the pebbles.

FIG. 204.—Young dunes, Blakeney, Norfolk, showing collection of sand behind young plants of the Marram-grass. Older stages are seen in the background. [Photo. E. J. S.]

FIG. 205.—"Blow-out" in a dune, Blakeney, Norfolk. The dense covering of Marram-grass is seen in profile, whilst owing to the action of the wind the rhizomes are seen exposed below. [Photo. E. J. S.]

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and more complete. The foremost dunes in which the sand is still readily moved by the wind are spoken of as *shifting dunes*. Nearly all the plants found upon these are perennial and capable of repeated growth, when buried by the wind-borne sand. In the earliest stages the first small heap of sand usually collects around some object, such as a plant of the Marram-grass (*Psamma*, Fig. 204), the Sea Couch-grass (*Triticum junceum*), or, less frequently, the Lyme-grass (*Elymus*). As layer upon layer of the blown sand accumulates, the shoots of the Grasses become successively covered, but no sooner does this take place than they are stimulated to further growth, resulting in the formation of fresh tufts of leaves at the surface (cf. Fig. 206).

The same process goes on repeatedly, each fresh layer of sand thus becoming bound to those beneath, so that the enlarging dune is permeated by a skeletal system formed of the branched rhizomes of the Grasses concerned. In this way the whole is knit together and a certain degree of stability is imparted to the extremely mobile soil-particles. Fresh sand will always tend to collect on the side away from the direction of the prevailing winds, owing to the shelter which the plants and, in later stages, the dunes themselves afford. If strong winds obtain for any length of time in a contrary direction, a considerable quantity of the accumulated sand may be removed and in this way " blow-outs " (*i.e.* excavations in the dune) will be produced, exposing to view the repeatedly branched rhizomes of the Grasses (Fig. 205), the older parts of which are, however, dead.

Other plants that act as sand-binders are the Sea Holly, Sea Convolvulus (*Convolvulus soldanella*), Sand Fescue (*Festuca arenaria*), and Sand Sedge (*Carex arenaria*), the last two, by virtue of their horizontal creeping rhizomes, tending more especially to bind together the surface-layers. The drift-line at the foot of the dunes, with its abundant humus, is usually inhabited by the Sea Rocket, Prickly Saltwort (*Salsola*), and Orach (*Atriplex*).

On the slightly older and more *fixed dunes* numerous shallow-rooted and short-lived annuals are generally to be found, especially on the lee side. These pass through their life-cycle in the winter and spring, whilst surface-moisture is plentiful, and dry up before the advent of summer. Examples are furnished by two species of Mouse-ear Chickweed (*Cerastium*

tetrandrum and *C. semidecandrum*), Lamb's Lettuce (*Valerianella*), Whitlow-grass, Lesser Cudweed (*Filago minima*), and the Sand Cat's-tail Grass (*Phleum arenarium*). Unlike the perennials, these do not exhibit repeated growth, but this is the less essential, not only on account of their short duration, but also because the superficial moisture during the few months of their exist-

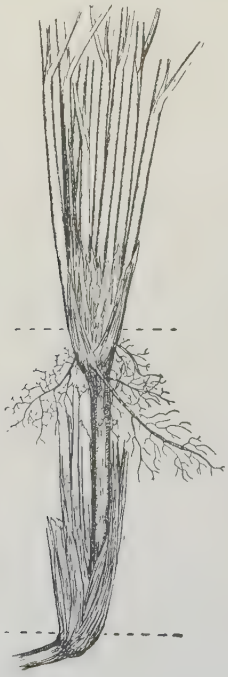

FIG. 206.—Portion of a plant of the Marram-grass (about one-half natural size), showing leaf-production at successive levels of dune-surface, these levels being indicated by dotted lines.

ence tends to "lay" the fine sand at the surface, which latter they themselves protect against the wind.

As the dunes become more stable other plants, less tolerant of mobile sand, begin to appear upon the lee face, gradually creeping to the windward side as this becomes sheltered by the dunes in front. Amongst such plants are the Stone-crop (*Sedum*), Lady's Bedstraw (*Galium verum*), Ragwort, Stork's Bill

(*Erodium*), Bird's-foot Trefoil, Burnet-rose, Mouse-ear Hawkweed (*Hieracium pilosella*), Red-seeded Dandelion (*Taraxacum erythrospermum*), Small Forget-me-not (*Myosotis collina*), and various Thistles. At a relatively advanced stage in dune-fixation numerous Lichens (*e.g.* Reindeer-moss, *Peltigera*) appear and their presence gives the sand-hills a general grey colour. Hence fixed dunes are sometimes spoken of as *grey dunes*, in contrast to the mobile or *yellow dunes*. Eventually a scrub may form upon the dunes in which the Sea Buckthorn (*Hippophaë*), Elder (*Sambucus*), Bittersweet (*Solanum dulcamara*), Brambles, and occasionally the Creeping Willow (*Salix repens*), are conspicuous forms.

The plants inhabiting the dune are practically all xerophytes with rolled leaves (*e.g.* the Grasses, cf. p. 176), fleshy leaves (*e.g.* Stone-crop, Sea Convolvulus), very hairy leaves (Sea Buckthorn, Stork's Bill), spines (Sea Holly, Sea Buckthorn), sunken stomates, etc. This xerophytic habit is due not only to the dry character of the soil, but also to exposure to winds and the strong heating of the surface-layers of the sand on a sunny day. Most of the perennials, as well as a few of the annuals inhabiting the dune, have deep and extensive (cf. p. 72) roots which thus reach the moisture, since the dry and powdery surface forms a mulch (cf. p. 70) preventing loss by evaporation from the layers below. Moreover, the strong heating of the surface involves great radiation at night, so that an extensive deposition of dew often takes place, and this forms the chief source of moisture of the shallow-rooting forms. The thick cuticle of many of the dune-plants not only prevents excessive transpiration, but also protects them from injury due to impact of sand-grains.

It may be added that some of the plants (*e.g.* the Stork's Bill) on the more stable dunes also flourish on ordinary inland soil, but the sand-forms usually differ from the normal type in having deeper roots, more hairy leaves, and foliage more closely adpressed to the soil.

In the more sheltered situations along the shore (*e.g.* bays and estuaries) large tracts of mud, or mud and sand, intersected by water-channels, frequently accumulate. Such areas which are periodically inundated by the tides constitute the habitat known as the *salt-marsh* (Plate VIII.). The first obvious

coloniser in these situations is usually the Marsh Samphire or Glasswort (*Salicornia*, Fig. 209) which, however, probably always follows small thread-like Seaweeds that have already to some extent bound together the surface-layers. On the south coast, especially that of Hampshire, the mud-flats are colonised by the Grasswrack (*Zostera*) and the Cordgrass (*Spartina*), the latter eventually forming a dense association like a maritime Reed-bed, whilst the former is of interest as being almost the only flowering plant inhabiting the sea round our coasts.

Colonisation by the Glasswort increases the rate at which silt is deposited, and the vegetation soon becomes less scanty owing to the arrival of several additional species, such as the Sea Plantain (*Plantago maritima*), Arrow-grass (*Triglochin*), Sea Aster (*Aster tripolium*), Sea Blite (*Suæda maritima*), and the Sea Manna-grass (*Glyceria maritima*). As further silt collects and the level of the marsh as a whole rises, the number of species, as well as the density of the vegetation, increases; in this intermediate condition (Fig. 207) the Sea Pink (*Armeria*), Sand Spurrey (*Spergularia media*), Sea Lavender (*Statice*), and Sea Mugwort (*Artemisia maritima*) are often found in abundance. Sandy salt-marshes are particularly characterised by the Perennial Glasswort (*Salicornia radicans*), Sea Milkwort, and Sea Heath (*Frankenia*), all found more especially towards the landward edge. The Silver Goosefoot (*Obione portulacoides*) sometimes invades the more sandy types of salt-marsh, first of all colonising the borders of the creeks (or water-channels) and then gradually spreading over the whole, until the former occupants are almost entirely driven out. In the final stage, when the level of the marsh is such that it is not covered even by the highest tides, a *salt-pasture* is formed, characterised by the presence of such Grasses as Bent-grass, Fescue, etc. Much of the flat land reclaimed from the sea occupies the former site of such salt-pastures (Fig. 208) which have been drained and cut off by dykes from the inroads of exceptionally high tides (spring-tides).

In many salt-marshes some of the plants occupy definite zones, corresponding to frequency of tidal inundation, a feature which is very pronounced where the Sea-rush (*Juncus maritimus*) and Sea Mugwort are present. These form fringes at the

FIG. 207.—Intermediate stage in salt-marsh formation, Hunstanton, Norfolk. The most conspicuous plant is the Sea Pink (in flower); the remaining vegetation consists of Glasswort, Sea Lavender, Sea Plantain, etc. On the horizon is seen a range of low sand-dunes. [Photo. E. J. S.]

FIG. 208.—Reclaimed salt-marshes, Bristol Channel. The flat-lying fields in the middle distance have been reclaimed from the sea. The dark areas in the distance, just beyond the shore-line, are salt-marshes in an early stage of colonisation. [Photo. E. J. S.]

[*To face p.* 346.

upper edge of the marsh, the former conspicuous by its height, the latter on account of its white hairy leaves.

The soil of a salt-marsh naturally contains a large amount of salt, this being particularly great when evaporation takes place during intertidal periods, and relatively small when the salt becomes washed out by heavy rainfall in the interval between the higher tides. The succulent character of many of the plants inhabiting salt-marshes is due to the development of large numbers of water-storing cells (cf. p. 180). This is well seen in the Glasswort (Fig. 209) in which the opposite leaves en-

Fig. 209.—Small plant of the Glasswort (about two-thirds natural size).

sheathe the stem and give the plant a jointed appearance, the flowers being embedded in threes in the tissue of the shoot (cf. the figure). This succulence appears to be related in some way to the presence of salt in the soil, since a considerable number of plants develop a similar fleshy habit when growing in saline situations (*e.g.* Bird's-foot Trefoil, Stag's-horn Plantain). The majority of salt-marsh plants are perennials, although the Glasswort and Sea Blite are annuals.

A few words may still be added on the *colonisation* of new ground. Wherever fresh soil is exposed (*e.g.* railway embank-

ments, quarries, Fig. 210, rubbish-shoots), it sooner or later becomes covered with vegetation, in the process of which a number of successive stages are always recognisable. Very frequently small Lichens, Mosses, and similar organisms constitute the first arrivals and, particularly where the soil is sandy or rocky, play an important part in providing the first-formed humus.

The first flowering plants to appear, either simultaneously

FIG. 210.—Colonisation of a disused quarry, Yorkshire. In the foreground are Ferns, Furze, Brambles, Wood-sage, etc. The barer parts are only occupied by Mosses and Heather. In the background are bushes of Broom. [Photo. E. J. S.]

with or subsequent to the Mosses and Lichens, are annuals, ephemerals, or biennials (often weeds) growing in the adjacent districts and possessing a good dispersal-mechanism (*e.g.* Shepherd's-purse, Fig. 1, Groundsel, Thistles, Charlock, Field Speedwells, Annual Meadow-grass, etc.). The broken surface of arable land (cf. p. 327) may be said never to get beyond this phase, so far as its wild flora is concerned. In later stages an increasing number of perennials are found, these gradually ousting the annuals by competition and naturally appearing

in an order roughly corresponding to the efficiency of their means of dispersal (*e.g.* Grasses, Willow-herbs, numerous Compositæ, Creeping Buttercup, Dead-nettles, Knot-grass, etc.).

In early stages the vegetation is open, *i.e.* there are considerable areas of bare ground between the plants, which latter are few as regards the number of species. Subsequently the vegetation becomes denser and denser, and for a time we have a relatively large number of forms battling for supremacy, until eventually the successful ones alone hold the field, these being

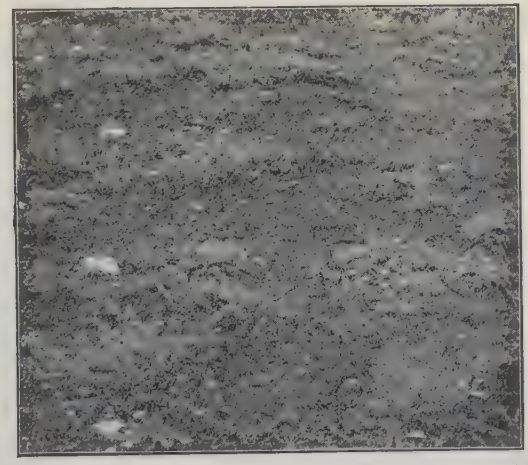

FIG. 211.—Colonisation of burnt heath, Hindhead, Surrey. The vegetation consists largely of the sprouting stumps of the Dwarf Furze (*Ulex nanus*). [Photo. W. B. Johnson.]

mainly perennials. If the soil remain undisturbed, shrubs and trees will after some time begin to assert themselves (Fig. 210), and thus we may ultimately get a dense scrub, analogous to that described on p. 321. A similar succession from an open to a closed association has been noticed above in our description of sand-dunes and salt-marshes.

A somewhat analogous series of phases can be observed after the coppicing of a wood or the devastation of a heath by fire. In these cases two factors come into play, viz. colonisation and sprouting of the underground parts of the woody plants. We may take the reclothing of a burnt Ling-heath as an example.

In the first years after a fire a considerable number of species (Rose-bay Willow-herb, Wood-sage, Tormentil, Milkwort, etc.) appear in large quantity; subsequently as the new shoots sprouting from the shrubby members of the heath-flora (Gorse, Fig. 211, Heather, etc.) assert themselves, these earlier colonisers become more and more crowded out, until finally the original condition is again attained.

CHAPTER XXVIII

Different Forms of Plant-Life

In the preceding chapters of this book we have almost entirely confined our attention to the flowering plants which, owing to their very complex structure and mode of reproduction, are generally regarded as the most highly developed forms. But there are an enormous number of non-flowering plants, of which some are relatively simple, whilst others exhibit an increasingly elaborate structure. Thus, Conifers and Ferns show certain resemblances to the flowering plants, whilst Mosses, Lichens, and Seaweeds present much more numerous points of difference. A brief consideration of these various types of plant-life will therefore help towards a comprehension of the Vegetable Kingdom.

The flowering plants are classed as Angiosperms and constitute one of the two great groups of the Phanerogams. The other group, viz. the Gymnosperms, includes as its chief representatives the Conifers. These, as we have seen, are all either trees (Fig. 39) or shrubs, monopodial in growth (p. 75), very commonly evergreen (p. 16), and possessing xerophytic foliage (cf. p. 175). We may take the Scotch Fir (*Pinus sylvestris*) as an example. This, like many other Conifers (*e.g.* Cedar, Larch), possesses dwarf-shoots (cf. p. 78 and Figs. 212, 213) arising in the axils of scale-leaves (Fig. 213, *s.l.*) and bearing the needle-like foliage leaves in pairs (Fig. 213, *d.s.*), long shoots being usually produced only at the beginning of each season's growth (cf. p. 78).

The reproductive organs are borne in so-called *cones* which are of two kinds, male and female, both occurring on the same plant. The former are evident towards the end of May as conspicuous yellow clusters composed of small egg-shaped

structures, each of which takes the place of a dwarf-shoot (Fig. 212 ♂) and represents a single male cone. These cones consist of a central axis bearing numerous leaf-like organs, to the under side of which a pair of large pollen sacs is attached (Fig. 213 D, *p.s.*).

The copious pollen is carried by the wind to the female cones which appear as small reddish bodies, about one-third of an inch in length, borne just beneath the terminal bud of the newly formed shoot (Fig. 213 A, upper part). The central axis

FIG. 212.—Portion of a branch of the Scotch Fir, bearing a cluster of male cones (♂) on the lower part of the year's growth (natural size). Near the top of the latter are seen, closely crowded, a number of immature dwarf-shoots.

of the female cone bears numerous paired structures, the lower member of each pair (Fig. 213 B, *L.S.*) being small and scale-like, whilst the other which is relatively large and thick (Fig. 213 B, *U.S.*) carries two small ovules (Fig. 213 B, *O*) on its upper surface. Some of the pollen is blown between the scales of the female cone and, on reaching the ovule, puts out a pollen-tube (cf. p. 250), which conveys the fertilising male element.

The actual process of fertilisation is deferred until the subsequent season so that, during the summer, cones of two ages

are to be found on a Scotch Fir (Fig. 213 A), viz. those just pollinated (the upper in the figure), and others just fertilised (the lower one in Fig. 213 A), but pollinated in the late spring of the previous year. The latter shed their seeds in the autumn, the empty brown cones, with widely separated scales, often remaining attached to the parent-tree for some time. The

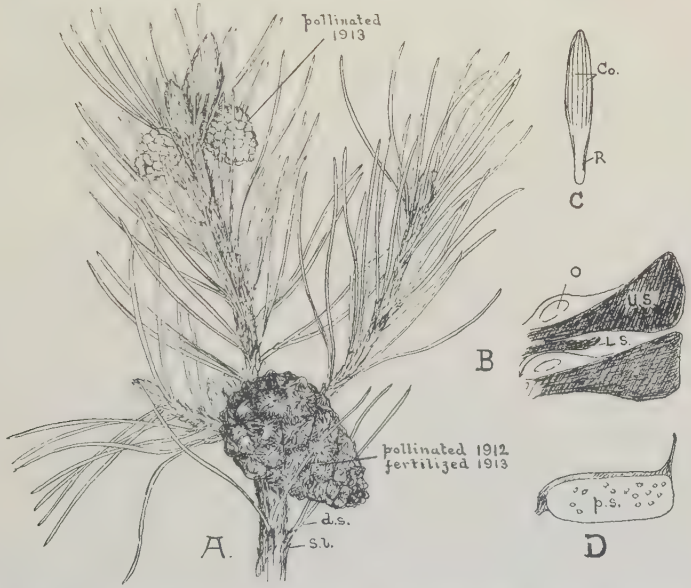

FIG. 213.—The Scotch Fir. A, Branch bearing female cones of two ages (about one-half natural size). *d.s.*, dwarf-shoot; *s.l.*, scale-leaf. B, Scales and ovules from a young female cone, cut through lengthwise (much enlarged). *L.S.*, lower scale; *O*, ovule; *U.S.*, upper scale. C, Embryo, dissected out of a ripe seed (enlarged). *Co.*, cotyledons; *R*, radicle. D, Single stamen from a male cone, in longitudinal section, showing one of the large pollen sacs (*p.s.*) (much enlarged).

winged seeds are albuminous (cf. p. 30), but are peculiar in having an embryo with numerous epigeal cotyledons (Fig. 213 C), the method of germination being very much like that of the Castor Oil or Sunflower.

It will be noticed that the chief difference between the Gymnosperm and the Angiosperm lies in the fact that the ovules of the former are not enclosed in an ovary (see p. 244),

but there are other distinctions, most of which are beyond the scope of this book (cf., however, p. 113).

The Ferns belong to a second great subdivision of the Vegetable Kingdom, known as the Pteridophyta which also include the Horsetails (Fig. 96 A) and Club-mosses. This subdivision, like the Phanerogams, is characterised by the possession of woody strands which are, however, absent in all the remaining groups. The Bracken (*Pteris aquilina*) is typical of most other Ferns and is found in abundance on many heaths and in woodlands. It possesses an underground stem with large pinnately compound leaves, a number of which appear

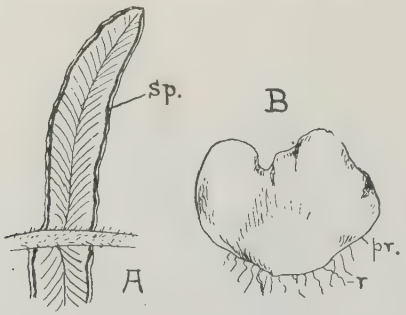

FIG. 214.—A, Small portion of a frond of the Bracken, seen from the under side and showing the line of sporangia (*sp.*) beneath the margin (natural size). B, A Fern-prothallus (enlarged). *pr.*, the prothallus; *r*, attaching hairs.

above the ground each year. The characteristic folding of the Fern-leaf has already been described on p. 98 (Fig. 52 A).

If the under sides of the pinnæ of the Bracken be examined in August, a narrow brown line will be found beneath the inturned margin of the blade (Fig. 214 A, *sp.*). A careful study with a lens shows that this line is composed of numerous capsules borne on short stalks, each such structure being spoken of as a *sporangium*. The latter contains a brownish dust resembling pollen, the individual grains of which are known as *spores*; these can be easily collected, if a ripe frond be shaken over a sheet of paper.

Wherever Ferns flourish in quantity (*e.g.* in conservatories), small flat green and more or less heart-shaped structures ($\frac{1}{8}$–$\frac{1}{4}$ inch in diameter) will be found growing on the surface

of the soil and on damp bricks. Each of these (a so-called *prothallus*, Fig. 214 B) has arisen from a Fern-spore and bears the male and female cells in special microscopic organs on its under surface. The male cells in the Fern, as in all groups below the Phanerogams, are capable of movement and swim, through the film of water between the prothallus and the soil, to the female cell which they fertilise.

As a result a young Fern-plant is produced which, for a short time, lives parasitically upon the prothallus; soon, however, it becomes independent, gradually increasing in size year by year till the mature condition is attained. Thus the Fern, in the course of its life-history, occurs in two forms, viz. the ordinary Fern-plant which produces the spores, and the prothallus which forms the sexual cells, each phase in its turn giving rise to the other. The Horsetails and Club-mosses show essentially the same course of reproduction as the Fern, but their sporangia are not borne on the ordinary foliage-leaves, but on scale-like structures collected together to form small cones (Fig. 96 A).

The most pronounced distinction between Pteridophyta and Phanerogams lies in the fact that two easily recognised individuals regularly alternate with one another in the life-history of the former; apart from this, the embryo in Pteridophyta grows continuously into the young plant, whereas in Phanerogams it develops to a certain stage and then remains dormant within the seed, *i.e.* there is a period of rest.

The next subdivision, the Bryophyta, comprises the Liverworts and Mosses, in both of which roots are absent. In the former group the plant frequently consists of a flat green branched structure, often with a somewhat thickened midrib (Fig. 215 A); a definite stem and leaves are not recognisable and such a simple plant-body is termed a *thallus*. In the Mosses, on the other hand, we have a small stem bearing minute leaves (Fig. 216 A). The internal structure, as compared with that of higher plants, is in both cases very simple, no true woody strands being present. Numerous minute hairs arise from the lower side of the thallus in the case of the Liverwort (Fig. 215 A, *r*), or from the base of the stem in the case of the Moss, these hairs serving both for absorption of moisture and to fix the plant in the soil.

All Bryophyta reproduce very extensively by vegetative propagation but, in addition, the plants at certain times produce sexual organs, similar to those formed by the Fern-prothallus. The female structures are difficult to locate without a microscope, but the male are often easily recognised. Thus, in the common Liverwort *Pellia*, numerous brown or blackish dots can often be observed along the midrib (Fig. 215 B ♂) and these mark the positions of the male organs. Similarly, in Mosses specimens are frequently found bearing a little flower-like rosette of reddish-brown leaves at the top of the stem, in the

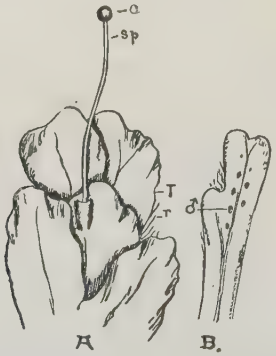

FIG. 215.—Thallus and reproductive organs of the Liverwort *Pellia* (about natural size). A, Thallus with a ripe sporogonium. B, Ditto with male organs (♂). *c*, capsule of sporogonium; *r*, attaching hairs; *sp.*, sporogonium; *T*, thallus.

midst of which are a number of dark dots, the male organs (Fig. 217 ♂).

The female cell, after fertilisation by the free-swimming male cell, gradually gives rise to a stalked capsule known as a *sporogonium* (Fig. 215 A, Fig. 216 A), within which is produced a powdery mass of spores. In the Liverwort *Pellia* the sporogonium is recognised in early stages as a swelling hidden beneath a little flap at the front end of the thallus, this swelling being due to the black capsule whose stalk at this stage is very short. When the spores are mature, the light-coloured stalk elongates rapidly and carries up the capsule (Fig. 215 A), the wall of which splits into four valves; in this way efficient dispersal of the spores is obtained.

In the Moss the sporogonium, as it is raised aloft on the elongating stalk, is at first covered with an often fringed hood (Fig. 216 B, *cp.*) representing the detached upper portion of the female organ within which the sporogonium commenced its development. If this hood be removed (Fig. 216 A) the capsule is seen to consist of a lower urn-shaped part (Fig. 216 A, *Ca.*), surmounted by a round lid (*l*). When a ripe capsule is examined, the lid is found to have become detached, exposing one or two rings of teeth (Fig. 216 D, *t*). The latter curl right back in dry air so as to leave the capsule open, but in damp air they

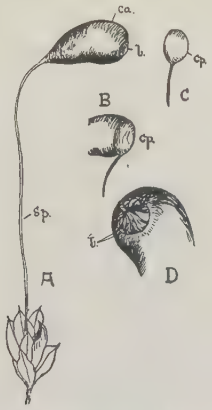

FIG. 216.—The Screw-moss (*Funaria*). A, Entire plant with sporogonium (somewhat enlarged). *Ca.*, urn of capsule; *l*, lid of same; *sp.*, stalk of sporogonium. B, Young capsule with covering hood (*cp.*) (enlarged). C, A detached hood (enlarged). D, Top of mature capsule (considerably enlarged). *t*, the teeth.

curve inwards so that the contained spores are protected. When the teeth are spread open, the spores are shaken out by the wind, much as the seeds from a Poppy-capsule (cf. p. 285).

In both Moss and Liverwort the sporogonium is the plant developed from the fertilised female cell; this sporogonium does not, however, become independent, but lives parasitically upon the individual bearing the sexual organs. The spores, on germination, give rise to new Moss [1]—or Liverwort—plants

[1] In the Moss the spores do not give rise directly to the new individual, but first to a richly branched green thread-like growth (the *protonema*) from which one or more Moss-plants are produced.

which in their turn produce sexual organs and, from the fertilised female cells, sporogonia. Here then, as in the Fern, we have a constant alternation between plants bearing sexual cells and others forming spores. But, whereas in the Fern the spore-producing plant is the more lasting and elaborate structure, in the Bryophyta it is the individual bearing the sexual cells that is most conspicuous and the more permanent of the two.

The lowest subdivision (Thallophyta) of the Vegetable Kingdom includes the Algæ and Fungi. To the former belong the Seaweeds and Pond-scums, and to the latter the Mushrooms, Toadstools, Moulds, and Mildews. The plant-body in these forms

FIG. 217.—Male plant of the Moss *Mnium* (enlarged), showing the apica rosette of leaves enclosing the male organs (♂).

is, as a general rule, much simpler than that of the Bryophyta, frequently consisting merely of a branched or unbranched thread of cells. This is the case in many of the Pond-scums, whose methods of reproduction can, however, only be studied with the aid of a microscope. Many of the Seaweeds are of much larger dimensions and we may take the Bladder-wrack (*Fucus vesiculosus*) as our type.

This plant which, as we have seen (p. 341), is very common between tide-levels, consists of a repeatedly forked thallus, each branch being traversed by a well-marked midrib (Fig. 218). The whole plant is firmly anchored to the rock by an adhesive disc at its base. At certain points on the thallus large swellings (Fig. 218, *b*) occur on either side of the midrib; these

are air-bladders which give the plant buoyancy and also perhaps act as reservoirs for an internal atmosphere (cf. p. 332).

Any part of the thallus that happens to get broken off can, if it be carried to a suitable situation, give rise to a new individual, but the Bladder-wrack also exhibits abundant sexual reproduction. At certain times of the year the ends of the branches swell up and exhibit numerous small circular projections (Fig. 218, *c*), in the middle of each of which a small dot (Fig. 218, *ap.*) can be recognised with a lens. The projections mark spherical cavities in the tissue of the thallus containing

FIG. 218.—Small portion of a thallus of the Bladder-wrack (about natural size), showing the fertile ends of two branches. *ap.*, apertures of cavities; *b*, air-bladder; *c*, cavity containing sexual organs.

the sexual organs (the male on one plant, the female on another), whilst the dots represent the apertures by means of which the cavities open to the exterior.

Both male and female cells are squeezed out of the cavities in a little mass of slime, when the thallus contracts during intertidal periods and, during the subsequent high water, fertilisation of the female is effected by the free-swimming male cells. The female cell thereupon gradually grows into a new Bladder-wrack.

Whereas the bulk of the Algæ occur either in fresh water or in the sea, a few are found in more or less dry situations, *e.g.*

the dense green weft of *Vaucheria* commonly seen on the soil of flower-pots. Further, the pale green powdery growth on tree-trunks, palings, etc. is generally due to the Alga *Pleurococcus*, an organism composed of but a single cell.

Amongst the Fungi, we have already referred to the weft of threads composing the plant-body in the Moulds and have seen that from this creeping tangle upright branches terminating in sporangia are frequently produced (cf. p. 144 and Fig. 78). The spores of such forms are remarkably resistant to all kinds of conditions and moreover are very light, so that they are to be found everywhere amongst particles of dust. Hence it comes about that on any suitable material (jam, bread, old boots, etc.), if left exposed, a rich growth of Mould soon appears.

As another example of a Fungus we may study a Toadstool (Fig. 219 A) in which (cf. p. 145) the actual vegetative part (the spawn) is underground and resembles that of a Mould, whilst the overground portion is the spore-producing structure. The spores are formed all over the surface of the radiating plates (gills, Fig. 219 A, *g*) on the under side of the cap (Fig. 219 A, *Cp.*). If the latter, in a ripe Toadstool, is cut off and laid with the gills downwards on a sheet of white paper, a brown print due to the shed spores is formed after a few hours.

A rather curious group of plants is that constituted by the Lichens which occur very commonly on tree-trunks, rocks, old walls, etc., appearing as closely attached discs or much branched structures, often of a greyish or bright yellow colour. The plant-body consists of both a Fungus and an Alga living in close association and deriving mutual benefit from one another. In most cases the bulk of the thallus is constituted by the densely arranged threads of the Fungus which completely encompass the algal cells within. Most Lichens develop little cups in which the spores are produced (Fig. 220, *fr.*), as in many Fungi.

The previous considerations have shown that, starting with simple forms like many of the Algæ, composed of but a single cell or of a mere thread of cells, we first pass to more elaborate types like the Liverworts and Mosses; from these we come to vascular plants, such as the Pteridophyta, till we reach the culmination of complexity in the Flowering Plants. We have seen in Chapter XXIII. that we can group plants to-

gether, so that the members of any one group resemble one another in numerous features, and it is reasonable to suppose that these have, at some period more or less remote, been derived from a common ancestor. In this way, by studying the various groups of plants and classifying them according to their apparent resemblances, we get an approximate estimate of their relationships. We thus obtain evidence for the belief that the first plants to flourish on the earth were simple forms like the Algæ and that from such, in the course of the ages, there have

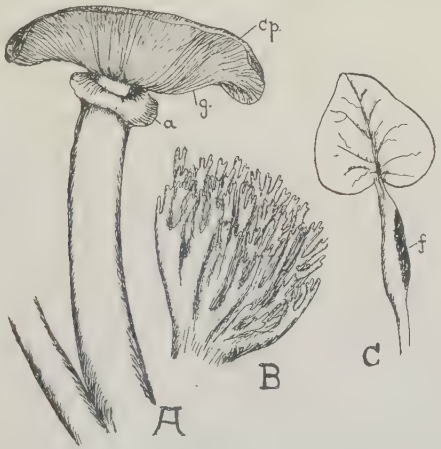

FIG. 219.—Fungi. A, A Toadstool (*Agaricus*) (slightly reduced). *a*, tissue representing the remnant of a continuous ring which in the young Toadstool covers over the under-surface of the cap; *Cp.*, cap; *g*, gills. B, Coral-Fungus (*Clavaria*). The spores are here produced all over the branched portion. C, Leaf of Lesser Celandine attacked by a Rust-Fungus (*f*).

gradually arisen more and more complex forms until ultimately the Flowering Plants were evolved. A study of the remains of plants preserved as fossils supports this view, since it shows that the Angiosperms did not appear on the surface of the earth till a relatively late epoch, the flora of earlier ages (*e.g.* the Coal Measure period) consisting largely of Fern-like plants and Gymnosperms.

Close observation will always lead to the conclusion that no two organisms are ever quite alike; just as the members of a

family differ in feature and character, so too the offspring of any plant vary amongst one another. Some of these variations, when pronounced, may render the form concerned more successful in the struggle for existence (*e.g.* may enable it to grow sturdier and to produce more offspring) and in this way a race having the particular characteristic may tend to become established. On the other hand a variation may be such as to make the organism less fitted for existence, in which case it will not generally survive in competition with other individuals not so modified. New forms of plants may thus ultimately arise, which may even be more successful than the parent-form, so that the latter will be ousted. In some such way we can imagine a gradual evolution of the Vegetable Kingdom, from simple to more and more complex forms, to have taken place, many of the intermediate types having disappeared through failure to

FIG. 220.—Thallus of a Lichen (natural size), showing the little spore-cups (*fr.*).

compete successfully with the better equipped forms that were slowly developed. As a consequence the plant-world at the present day, instead of showing a perfectly continuous chain of more and more complex organisms, exhibits a large number of more or less distinct groups of forms whose exact relationship with one another it is often very difficult to determine, since many of the links in the chain of evolution are missing.

In horticulture many new forms of plants have been produced by the propagation of marked variations (so-called *mutations*), though in some cases florist's varieties are obtained by the crossing of one plant with a closely related form, the pollen of the one being transferred to the stigma of the other. In this way *hybrids* result, the offspring of such a union being usually more or less intermediate between the two parents, though sometimes resembling neither. It is probable that new forms have arisen in both these ways in the course of evolution

APPENDIX

I. *Iodine-solution.*—It is best to use a solution of Iodine in potassium iodide, made by dissolving a few crystals of the former in a strong solution of the latter and diluting with water to a light brown colour. Tincture of Iodine (*i.e.* a solution in alcohol), which can be obtained from any chemist, will answer almost as well.

II. *Demonstration of importance of micropyle for absorption of water* (*second method, after Osterhout*).—A number of slots are cut into the edges of two large corks and into these, dry Beans are wedged in such a way, that those in the one cork have their micropyles directed upwards, whilst those in the other have them directed downwards. The corks are now placed on the scale-pans of a balance and nails or pins are inserted into the lighter, till both are of equal weight. Thereupon the corks are allowed to float on water for a day, when subsequent weighing will show that the seeds with the micropyles dipping into the water have taken up far more moisture than the other set.

III. *Boxes for experiments on growth of plumules and radicles.*—The sloping glass-front can be fixed in position by means of two pieces of wood nailed either side of each end. For this purpose two narrow rectangular strips of wood are sawn through diagonally and the glass placed between the sawn edges (see wood-supports in Figs. 21 and 29).

IV. *Method of obtaining seedlings with straight radicles and plumules* (Fig. 221).—A flat seed-box is filled with moist sand, in the surface of which are embedded rows of soaked seeds parallel to the long sides of the box. The seeds must be so placed that their radicles are all directed towards the same side and lie parallel to one another; about 2 inches should be left between the successive rows (Fig. 221). The box is

covered, either with a sheet of cardboard or a piece of wood which is merely tied on, so as to be readily removed. The whole is then stood on one of its edges, with all the radicles pointing downwards. A very considerable proportion of the seeds will be found to develop straight radicles and plumules (Fig. 221).

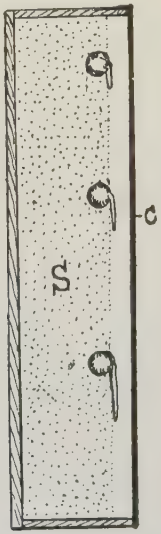

FIG. 221.—Section of box to show method of growing seedlings with straight plumules and radicles. *S*, sand; *C*, cover of box.

V. *Method of marking radicles or plumules with Indian ink.*—The marking may be most conveniently carried out by using a piece of cotton stretched out on a short piece of bent fish-bone like an archer's bow. The radicle or plumule is laid along the edge of a ruler and the marks are made by the stretched cotton which is moistened with Indian ink.

VI. *Water-bath.*—A simple form may be constructed by heating a large beaker, having a spout and three-quarters full of water, on a sand-bath, a large evaporating dish being placed over the mouth of the beaker. The soil, etc., is put into the dish and will thus be exposed to a temperature of about 100° C.

VII. *Attachment of rubber tubing in an air-tight manner.*—The

internal diameter of the tubing should be somewhat smaller than the diameter of the object to which it is to be attached. Moistening with water will make it easier to slip the tubing over the object. To ensure an air-tight connection, thin wire may be firmly twisted around the points of junction.

VIII. *Recovery of a flaccid shoot when water is sucked into it.*—This may be demonstrated with the help of the apparatus shown in Fig. 62 (p. 113), by using a one-holed rubber cork on the flask, provided with a piece of glass tubing bent as in the figure. The upper end of the flaccid shoot is removed and the cut surface, thus produced, is attached to the long arm of the glass tube, whilst the lower end of the shoot is placed in a tumbler of water. In order to prevent the entry of air into the tissues by way of the stomates (cf. p. 116), both surfaces of the flaccid leaves should be vaselined. As a consequence, the suction generated within the flask (as described on p. 114) operates in causing a rapid flow of water through the shoot. After a short time the leaves become turgid.

IX. *Graduation of scale in apparatus shown in Figs.* 55 *and* 107.—The apparatus is laid down horizontally, with the pointer at the base of the scale, and an inch-ruler is placed vertically (*i.e.* parallel to the support) against the end of the short arm of the lever. This latter is then moved through successive eighths or quarters of an inch and the corresponding positions of the pointer on the arc (*a*) marked off.

X. *Method of blowing out an egg.*—In pricking the egg care must be taken to pierce the membrane of the yolk. A bent glass tube drawn out into a long pointed nozzle is then loosely inserted; by blowing through the tube, the hole in the egg being directed downwards, the contents are caused to escape gradually, till the shell is empty.

XI. *Method of filling a narrow tube with liquid* (Fig. 222 A).—A fine glass-tube is attached to a small funnel and inserted into the tube to be filled, so as to reach to its base. The liquid is then poured into the funnel and, as the wider tube fills, the narrower one is withdrawn (Fig. 222 A). This method is also applicable to the filling of an egg-membrane (p. 107).

XII. *Method of passing a branch through a hole in a rubber cork* (after Osterhout, Fig. 222 B).—A cork-borer, wide enough to take the branch, is passed through the hole in the cork, in the opposite direction to that in which it is desired to insert the branch. The latter is pushed some little way into the

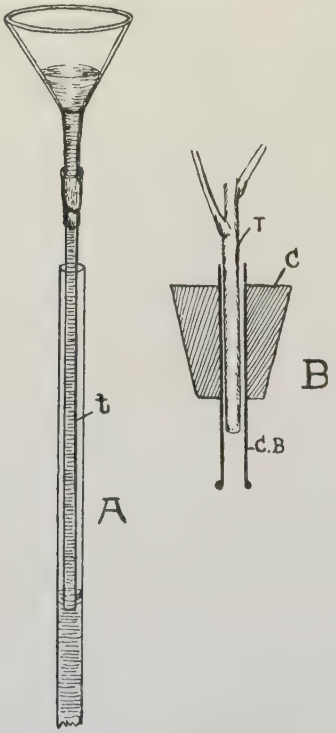

FIG. 222.—A, Method of filling a narrow tube with liquid. *t*, glass-tube filled with water and attached to funnel. B, Method of passing a branch through a hole in a rubber cork (after Osterhout). *C*, cork; *C.B.*, cork-borer; *T*, shoot.

borer (Fig. 222 B) which is then slowly withdrawn, thus leaving the branch in the cork.

XIII. *Analysis of the ash.*—The presence of a few of the elements can be detected very simply. Thus, if a clean Platinum-wire be moistened with hydrochloric acid, dipped into the ash,

and held in the non-luminous flame of a Bunsen burner, the yellow colour indicates the presence of Sodium. If the flame is viewed through a piece of blue Cobalt-glass, the violet colouration due to Potassium is recognisable. If the ash is boiled with water, the filtrate, after being acidified with hydrochloric acid, gives a white precipitate with barium chloride, thus indicating the presence of Sulphur in the form of sulphates. A portion of the filtrate treated with an equal amount of dilute nitric acid, followed by an excess of ammonium molybdate solution, gives on boiling a yellow precipitate due to the presence of phosphates.

XIV. *Sand-cultures.*—In place of the water-cultures, sand-cultures may be prepared in the following way: A quantity of silver sand is strongly heated for some time and allowed to cool again. After this, boiling water is allowed to drain through it several times in succession. The sand is then placed in small pots which are watered daily with the different kinds of culture-solutions. For such experiments it is advisable to employ plants which readily grow in a sandy soil, such as Poppy or Cress.

XV. *Additional precautions to be used in water-cultures.*—If such cultures are continued for some time, it is advisable to renew the culture-solution every few weeks. Should the roots begin to show a growth of Moulds or Bacteria, the latter should be carefully removed with a fine brush; to prevent a growth of this kind on the under sides of the corks, the latter should be charred. Large jam-jars are well suited for the experiments, whilst as regards plants Maize, Wheat, Sunflower, etc. give good results.

XVI. *Culture-solutions lacking essential elements.*—For solution without Nitrogen, see p. 127. To make up one lacking Sulphur, substitute Magnesium nitrate for Magnesium sulphate. To eliminate Phosphorus, use Potassium sulphate instead of Potassium phosphate. For the solution without Calcium, employ Magnesium nitrate in place of Calcium nitrate, and for the one without Potassium, substitute Sodium for the Potassium salts.

XVII. *Spectroscope.*—A cheap form of direct-vision spectroscope can be obtained, at a price of from about fourteen shillings upwards, from the various firms selling physical apparatus

Such instruments consist of a short telescope-tube with a narrow (generally adjustable) slit for the entry of the light at one end and an eye-piece at the opposite end. Between the two lie several prisms which serve to break up the band of white light, entering through the slit, into its component colours.

XVIII. *Method of covering leaves with stencil-plates.*—The stencil-plate is placed on the upper side of the leaf, whilst a piece of cardboard of equal size and perforated by a number of small holes is fixed in a corresponding position on the lower surface. The two structures can be kept in position by fastening them with spiral paper-clips.

XIX. *Starch-solution.*—Mix a little powdered starch with cold water and stir until a thin paste is obtained; then add about a pint of boiling water, when a thin opalescent starch-solution results.

XX. *Proteid-reactions.*—It is well to repeat the tests described on p. 170 with a solution made by shaking up a little white of egg (unboiled) with water.

XXI. *Auxanometers.*—The instrument described on p. 195 can be obtained from Messrs. Flatters & Garnett, 309 Oxford Road, Manchester, at a cost of about thirty-five shillings. A rather more expensive instrument, known as Farmer's Auxanometer, can be purchased for about £3 from any scientific instrument dealer. This instrument has a cylindrical drum which for use is covered with smoked paper and admits of readings being taken every quarter, half, or whole hour. Readings at such short intervals are, however, quite unnecessary for elementary experiments.

XXII. *Klinostat.*—A simple klinostat (Farmer's) can be purchased for about twenty-five shillings from any scientific instrument dealer. The instrument described on p. 205 can, however, be made at a cost of about three shillings.

XXIII. *Models of flowers.*—In the study of pollination-mechanisms it is instructive to make models of the flowers concerned. For this purpose a large bottle-cork can be used as the floral receptacle, and the petals, or corolla (if gamopetalous), cut out of white paper and pinned to it in the appropriate positions.

The stamens and style can be made of wire pushed into the cork below and bearing pieces of Elder-pith or Carrot to simulate anthers and stigma. A rough model of an insect may be constructed from cotton-wool, with a piece of wire of suitable length attached at one end to represent the proboscis. Both flower and insect should be made on a much enlarged scale, their relative proportions being reproduced as faithfully as possible.

XXIV.—*Demonstration of change in stomatal aperture.*—A simple method of showing this is by means of the apparatus

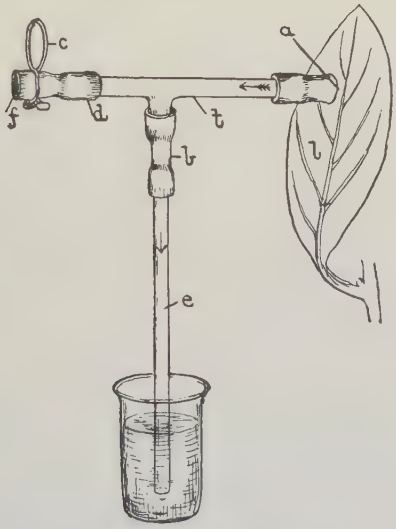

Fig. 223.—Porometer, for description see text.

known as the *porometer*. This may be constructed as follows (Fig. 223) :—A short length of stiff thick-walled rubber tubing (about ¼ inch bore) is cut off square, and one end is melted by placing it against a heated metal plate. On cooling, the melted end (*a*) is pressed against the under side of a leaf (*l*) still on the plant. The other end is connected with the arm of a glass T-tube (*t*). To the other horizontal arm is attached about two inches of thin rubber tubing (*d*), which is closed by a clip (*c*), and to the vertical arm of the T-tube a twelve-inch

glass tube (*e*) is connected at *b*, with its open end in a beaker of water. By opening the clip and applying suction at *f* the water is raised in *e*. The clip is now closed and the water-column in *e* will be seen to fall. This is due to the passage of air from the stomates of the uncovered part of the leaf through the air-spaces into the tube *t*. According as the aperture of the stomates is wide or narrow the water-column falls rapidly or slowly. By attaching a ruler to the back of *e*, the rate of fall of the water through a given distance can be estimated. In this way the effect of light and darkness, etc., can be compared.

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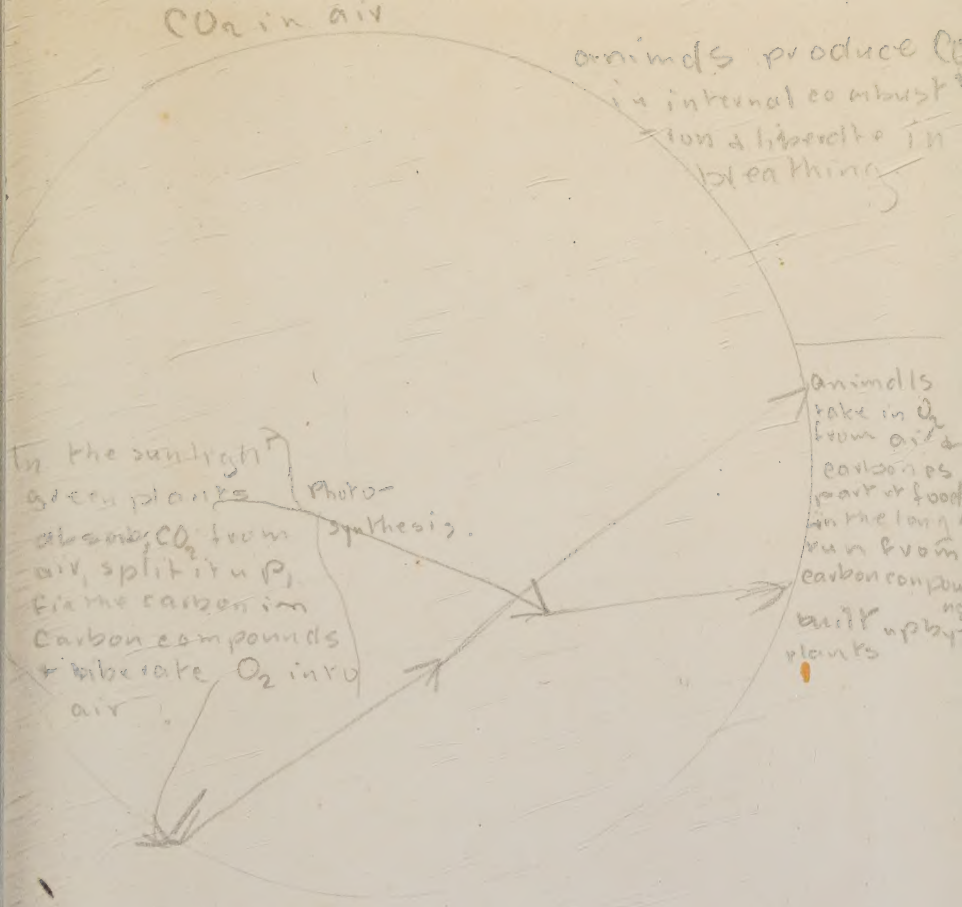
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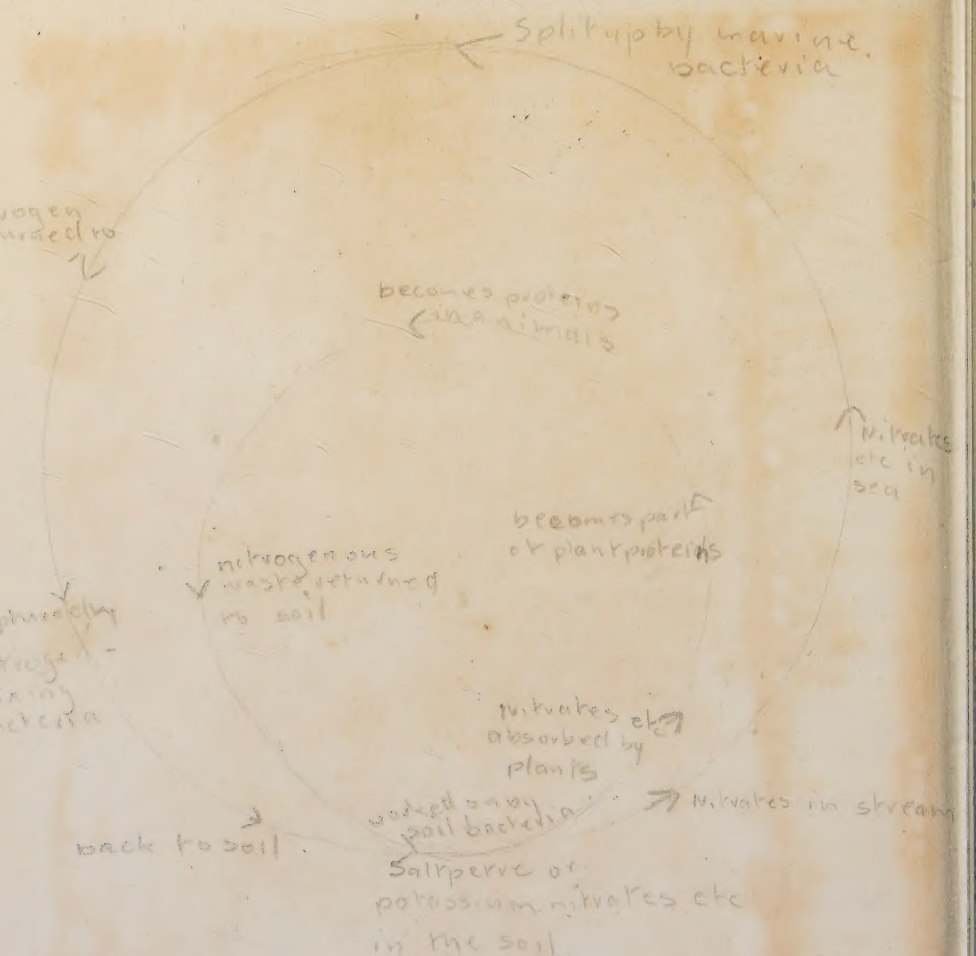
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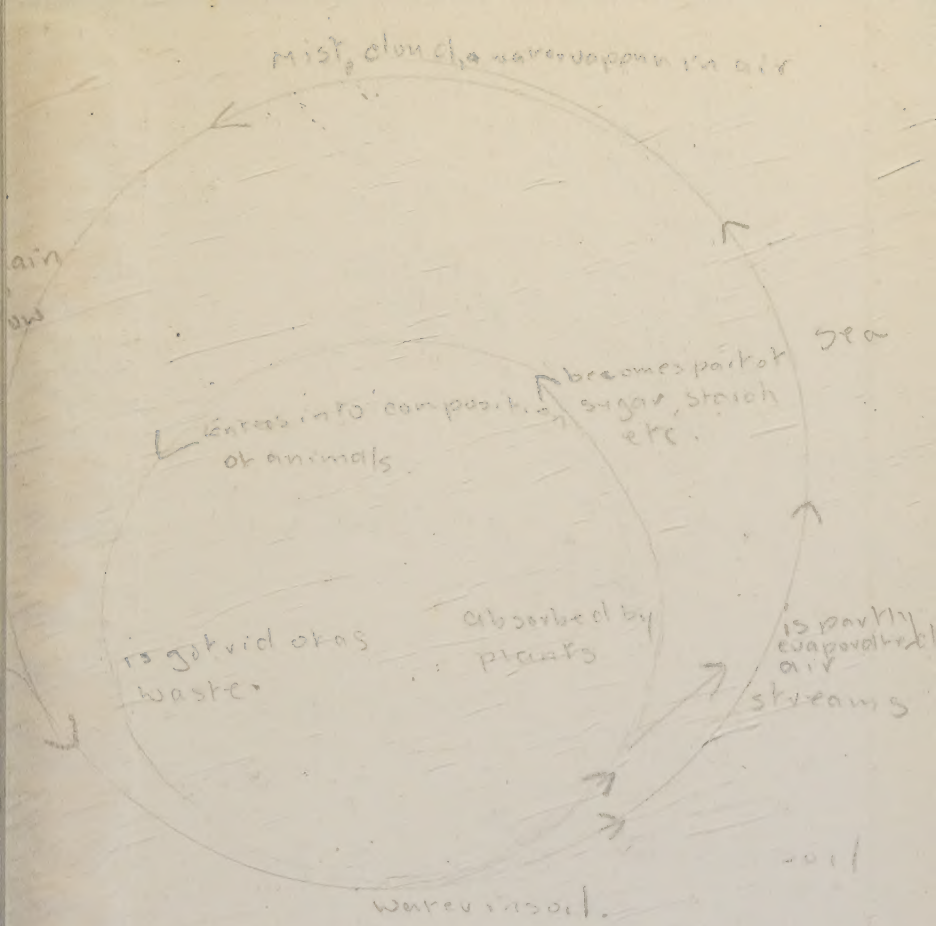

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